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THE VEGETATION OF SIERRA DE NIPE, CUBA

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THE VEGETATION OF SIERRA DE NIPE, CUBA

INTRODUCTION

Although the northeastern mountains of Cuba, including Sierra de Nipe, are far more interesting botanically than are many other endemic regions of Cuba, botanists unaccountably have concentrated their interest in the latter.

The first botanist to collect in Sierra de Nipe was Charles Wright, who was there for a few days in the summer of 1860. Wright's exploration and collecting in this region was limited to the calcareous slopes and limonite soil on the western part of this Sierra, very near to Cayo del Rey. Nevertheless his collecting here was not as intensive as were others made by him in other regions of Cuba.

J. A. Shafer was the second botanist to visit this region, making two trips, the first in 1909 and the second in 1912. As often happens, Shafer reached the locality accidentally while visiting some friends at the manganese mines at Woodfred, on the eastern slopes of Sierra de Nipe. Shafer's collecting was quite intensive, but far from complete.

The third botanist to visit the region was E. L. Ekman, who fortunately was established in "Bayate," a sugar mill, near the western slope of this Sierra from 1914 to 1917. Using this place as a base for his explorations, Ekman was able to visit Sierra de Nipe several times, making the most complete botanical exploration of those hills to date.

Since the time of Ekman, as far as we know, no other botanist visited the region until we collected there in 1939 and 1940. Since this time, several botanists have enjoyed trips through the superb vegetation clothing the serpentine and limonite soils of Sierra de Nipe (Fig. 1).

After exploring and collecting in almost every region of Cuba, we came to the conclusion that the northern mountains of Oriente are the regions of most endemism among plants of Cuba.

The purpose of this monograph is to describe the endemic vegetation of Sierra de Nipe. However, in view of the limited existing knowledge of the Cuban vegetation, we are forced in several sections of this paper to include a general discussion of the Cuban vegetation. The reader will find for instance a section dedicated to the different centers of endemism of Cuba, which at the same time stresses the importance of the endemism of Sierra de Nipe. Another section is a brief discussion of the "antillean montane forest," or the mountain vegetation of the West Indies, generally mentioned as rain forest. Also we present herein a new combination because of the importance of the species involved in its community.

In another section we comment on the inhabitants and agriculture of Sierra de Nipe, not, however, to make a biotic discussion, but for general information. The section on timber industry is included mainly for the purpose of showing the importance of the pine land in this region. Because of the lack of maps



FIG. 1. The limonite region of Sierra de Nipe. *Pinus cubensis* in the foreground.

and general geographical knowledge of Sierra de Nipe, we have considered it useful to discuss briefly the geography of this region. The ecological interpretation given in this paper is mainly based on physiognomy and edaphic factors, but observation of the distribution of the species and the floristic composition is taken into consideration.

This paper could never have been completed without the criticism of Dr. F. E. Egler of the New York State College of Forestry at Syracuse University, who also translated the original manuscript, written in Spanish. The criticisms of this paper given me by Dr. S. A. Cain of the University of Tennessee are gratefully acknowledge. I also want to acknowledge the valuable help of Mr. Otto Degener of the New York Botanical Garden and T/Sgt. J. C. Baart in reading manuscript and proofs.

GEOLOGY

During the late Jurassic and early Cretaceous, large strata of metamorphic rocks were deposited in Cuba, and at this time a great quantity of serpentine was introduced. During the upper Cretaceous, much of

Cuba was folded and much of it remained land during the late Cretaceous. From the Eocene to Pleistocene, most of Cuba submerged and emerged several times. Whether the northeastern part of Cuba remained elevated in these later periods as the southeastern part was, is not definitely known. In general we may say that the northeastern part of Cuba appears to have an ancient geological history and, according to Longwell, it is possibly the oldest region of the island. But because of the present inadequate geological knowledge of this area, the age of the northeastern part of Cuba is still unknown. If we follow Spencer and Rutten, it seems that the north shores of Cuba are part of the remnants of the arc which formed the northern part of the Antillean Continent. At least, the flora of the northeastern part of Cuba appears to indicate to us the possibility that in other geological periods the northern coast of Cuba extended farther than its present limits. This is shown by the presence of a group of endemic genera, as well as by a large number of endemic species in this region, that seem to be relicts. Such relicts possibly possessed a large distribution in the past and at the same time were represented by many more related species than those now existing. This appears to be confirmed when we study the vegetation of one of the oldest regions of Cuba, the northern part of Pinar del Río, where on serpentine and iron oxide soils, is found a flora which permits us to establish the only existing bond with the flora of the northeastern part of Cuba.

We also must recognize that the vegetation in islands which have suffered marked geological changes is rich in endemic species. This is true of most of the Larger Antilles, and Cuba is a good example. During this process of geological evolution, part of the vegetation may survive and, in addition, by isolation and gradual evolution, numerous neo-endemic and vicarious species may originate.

Much of the above expressed opinions, neither agrees with existing paleogeographic maps, nor with the general opinion of a large number of zoogeographers. The native plants now living in Cuba, however, should solve part of the question regarding the often discussed origin of the Antillean flora.

GEOGRAPHY

GENERAL PHYSIOGRAPHY

Cuba, by far the largest of the West Indies islands, is situated at the mouth of the Gulf of Mexico, and possesses a total area of approximately 45,570 square miles. Its length is approximately 785 miles along the axial line from east to west, and its width varies from 25 to 120 miles. The island of Cuba is somewhat crescentic in outline, with the convexity in general toward the northeast. The northern boundary of Cuba is about 155 miles south of Florida. It is 55 miles west of Haiti; 100 miles north-east of Jamaica and 130 miles from the Yucatan Peninsula. The island lies between the 20° and 23° parallels of north latitude, extending slightly beyond each, and between the 74° and 85° meridian of west longitude.

THE ADJACENT PLAINS OF SIERRA DE NIPE

The Sierra de Nipe arises from an extensive plain, which in the west extends to the sabanas of Holguín (Fig. 14), becoming narrow at the north between these mountains and the sea, and stretching eastward between the Sierra de Nipe and Sierra de Cristal. In the northern and western parts of these plains, and in the vicinity of Sierra de Nipe, the alluvial soil is rich and supports extensive sugar fields which supply a group of the largest sugar mills of Cuba. As is to be assumed, in order to cultivate these fields, it was necessary to destroy the original vegetation, so that today one may observe only certain small herbaceous plants along the roads and paths of the sugar plantations, among which the most common are *Phyllanthus nodiflora* and *Euphorbia heterophylla*. Along the brooks and rivers which cut these plains are often found large individuals of *Bucida buceras*, sometimes covered with *Tillandsia usneoides*. Other trees here are *Samanea saman* and *Roystonea regia*. In the herbaceous vegetation of the same sites, *Phyllanthus nodiflora* and *Polygala portoricensis* are predominant. The extreme west of the plain is very low and is usually covered with water; for this reason it is not used for the cultivation of sugar cane, but only for sporadic and irregular grazing. In these low parts of the plain the predominant tree is the *Copernicia hospita*, palm 2-4 m. high. Sedges and grasses represent the herbaceous vegetation. At the north, between the Sierra de Nipe and the bay of the same name, are found large sugar plantations, but farther to the east, and between Sierra de Nipe and Sierra de Cristal, where the large Río Mayarí flows, the plain is covered with a deep and rich soil and is still mainly uncultivated. Here the royal palm, *Roystonea regia*, has not been destroyed, and forms the finest palm stands in all Cuba.

THE SIERRA DE NIPE TOPOGRAPHY

The Sierra de Nipe has its main axis extending from north to south, a direction also maintained by the highest peaks of the range, of which the most outstanding are La Mensura, 1,000 m. high (Fig. 24); El Gurugú, 900 m.; La Estrella, 800 m., and La Bandera, 800 m. All of these mountains and peaks have, as a common base, a large tableland some 600 m. high, which is known as El Pinar de Mayarí (Figs. 24 and 25). The peaks do not occur along the center of the plateau, but are slightly displaced toward the west side, for which reason the western slopes of this range are steeper than those of the eastern side; for the same reason, the northern part is steeper than that of the southern.

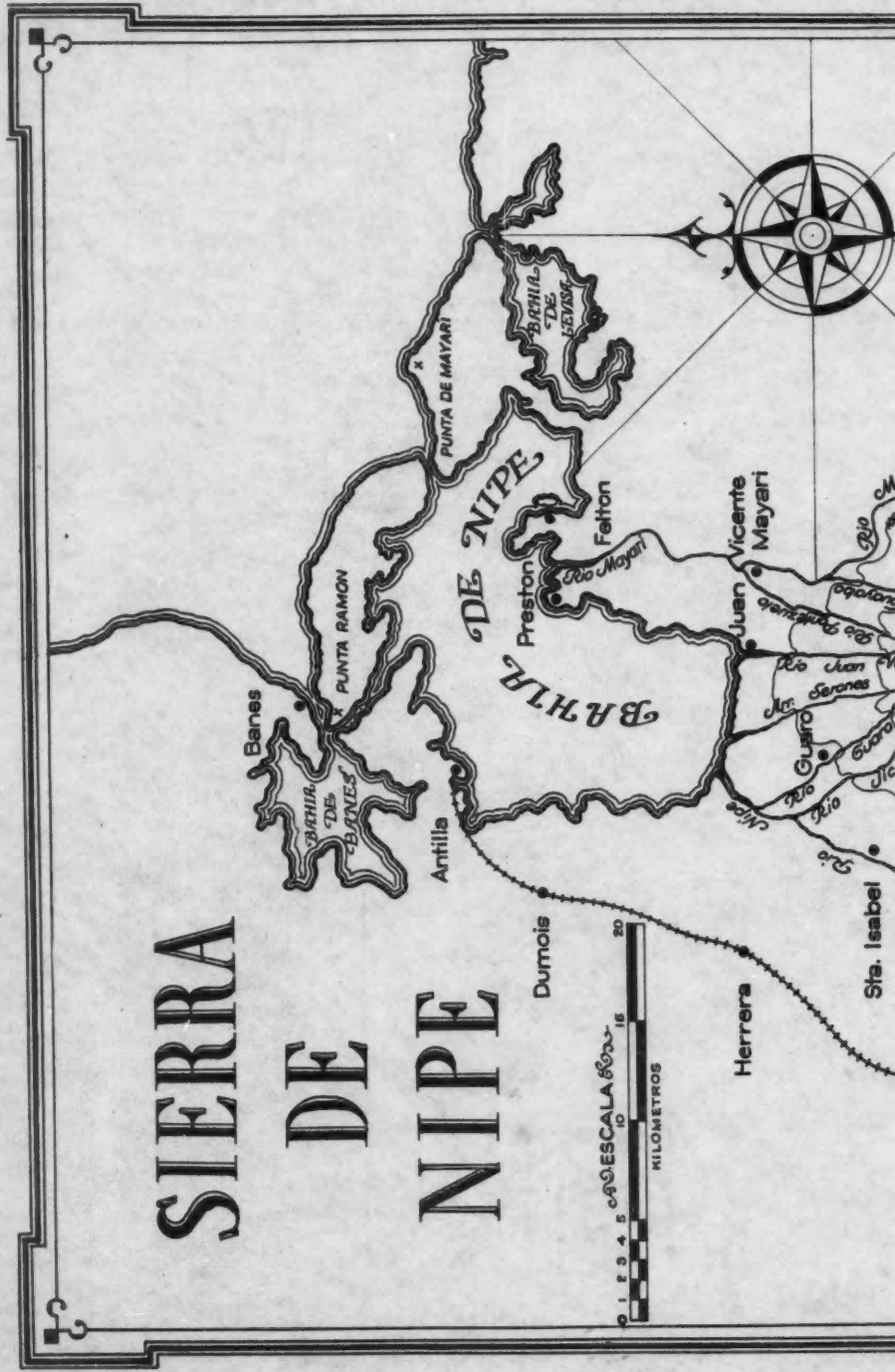
Because the western, northern and northeastern slopes of Sierra de Nipe are very steep, the brooks and rivers of these sides are more numerous and shorter than those of the south and southeast. For the same reason, it is not uncommon that many of the streams of the western, northern, and northeastern parts of the Sierra have rapids and water falls. The more noteworthy water falls are the Salto del Naranjo, and the Salto del Espíritu Santo, in the

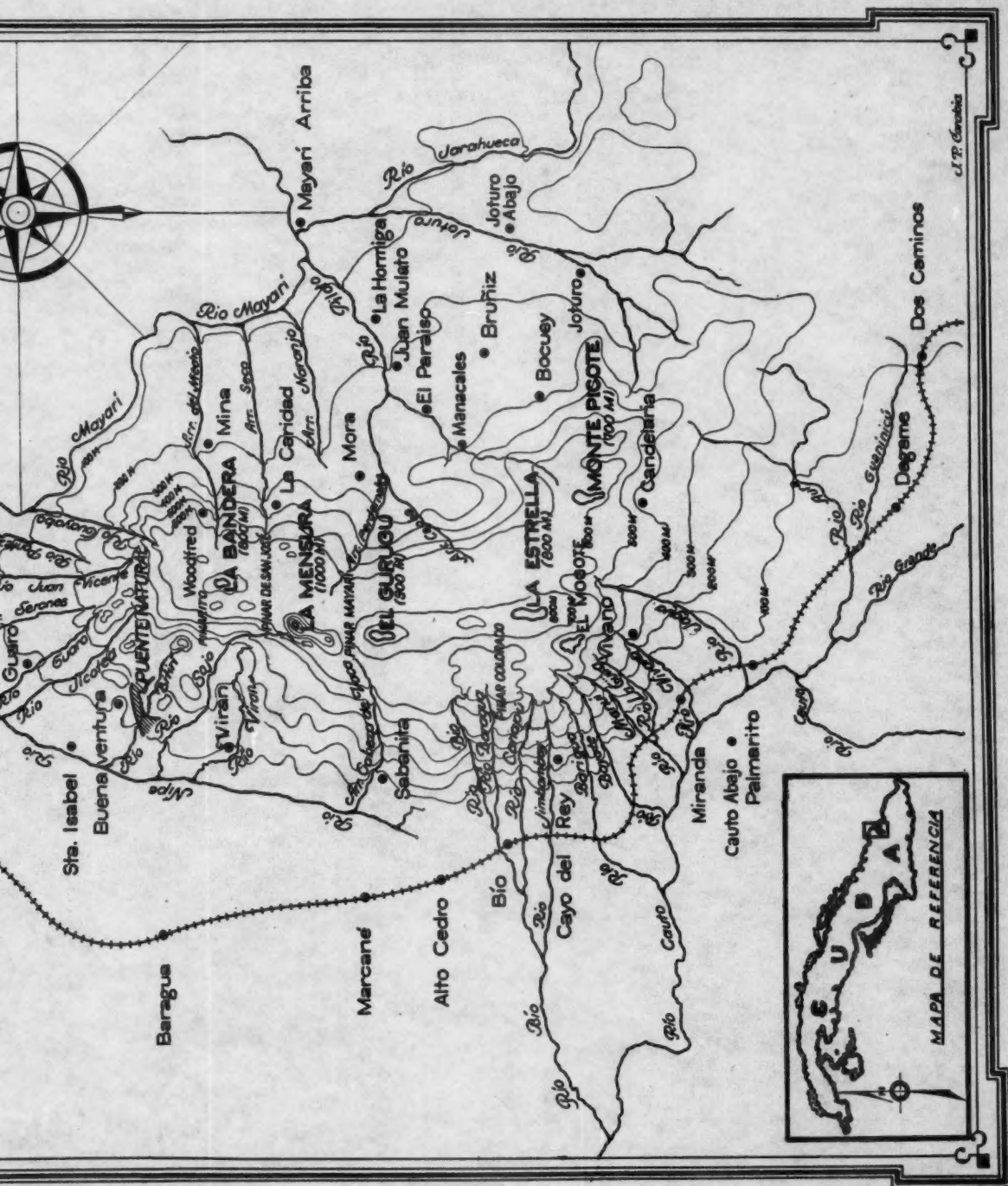
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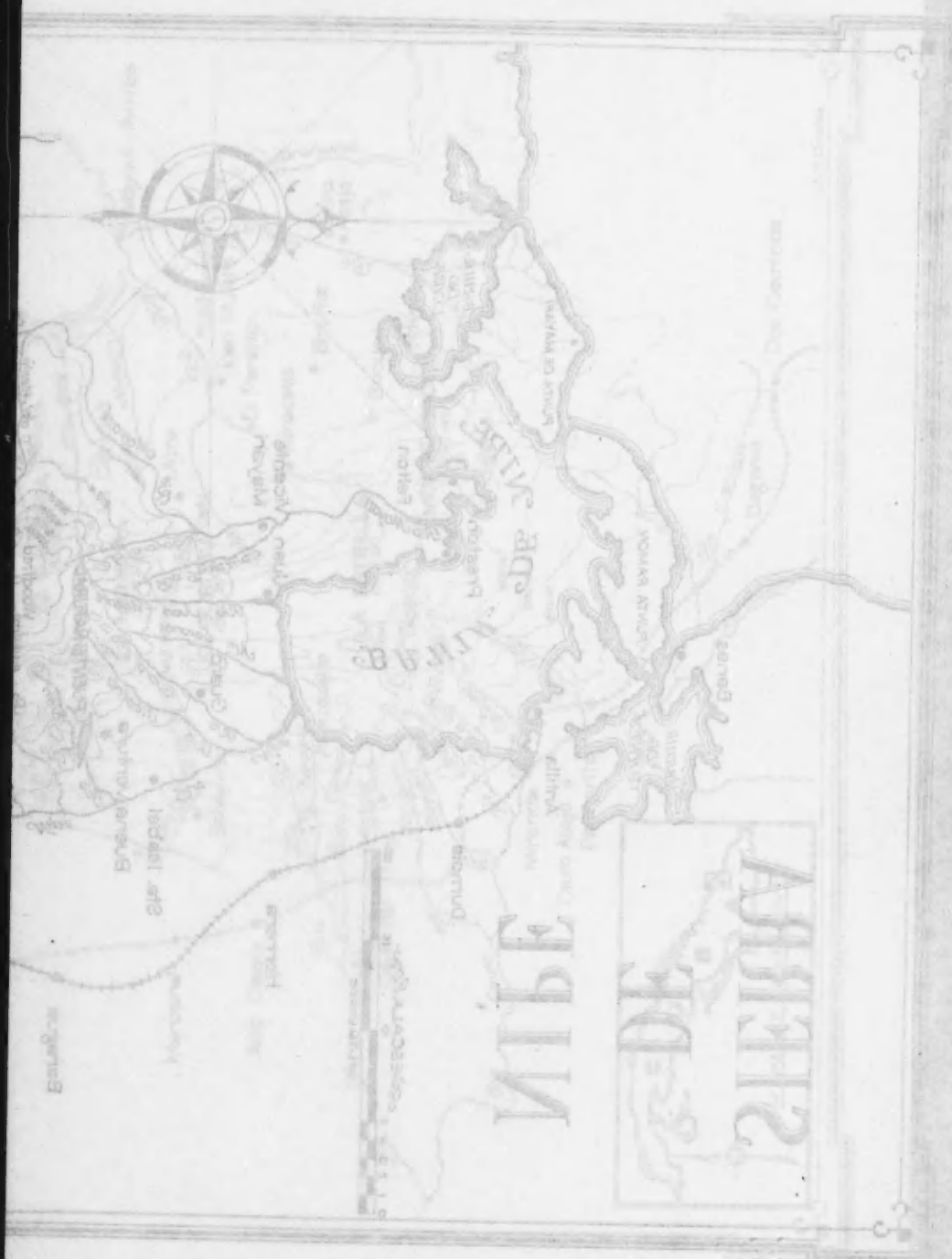
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SIERRA DE NIPE







northeast, the latter of which may be seen from the Bay of Nipe; in the west we have the Salto del Sojo, about 80 m. high (Fig. 20). The streams of the southwestern slopes of the range form the major upper watershed of the important Río Cauto, which is the largest river in Cuba, being some 300 kilometers in length. The other rivers of the western slopes flow into the Río Nipe, which in turn flows into the bay of the same name. Among the most important rivers of the western side of the range are the Río Viran, and the already mentioned Río Nipe. Another river worthy of mention is the Río Bitirí, which, in its course across the limestone region, has formed by erosion the interesting natural bridge of Bitirí (Fig. 2). Although in the south and southeast of the range, the rivers are neither numerous nor steep, they nevertheless, carry more water. The most outstanding among these is the Río Piloto, which like others in the vicinity, flows into the Río Mayarí, which in turn empties into the Bay of Nipe. The large Río Mayarí passes between the Sierra de Cristal and Sierra de Nipe, thus capturing all the waters of this part of the eastern coast. In the rainy season, the Río Mayarí attains considerable proportions, sometimes inundating completely the village of Mayarí situated near its mouth.



FIG. 2. Natural bridge over the Río Bitirí.

The water of the majority of the streams and rivers of Sierra de Nipe is pure and suitable for drinking, at least in the higher parts of the range. The waters of many of these streams possess medical properties due to their passing over serpentine rocks rich in magnesium. In the lower part, the rivers of the southeast, flow over permeable calcareous substrata dissolving appreciable amounts of calcium bicarbonate which in contact with the air and by evaporation become calcium carbonate. In this manner large deposits of calcareous tufa or travertine are formed, covering the streams and over which one may easily walk.

The Sierra de Nipe is surrounded by a limestone formation, forming at times almost perpendicular cliffs of about 80 m. high, which occur principally in the western part, between Miranda and Sabanita

(Figs. 12 and 14). At the east and south of the range, the limestone diminishes in height and in many parts it is entirely hidden beneath the vegetation. Included within the limestone frame, and forming the great central part of the Sierra de Nipe, are extensive areas of limonite and serpentine of more or less rolling topography (Fig. 7), culminating in a large central plateau of limonite (Fig. 24). In general the limonite dominates the higher parts of the range, while the serpentine is found principally covering the slopes of the hills and along ravines and rivers. Nevertheless, at other times bands of serpentine occur within the areas of the limonite, and sometimes the summits of the highest peaks are serpentine (Fig. 25).

SOILS

As described in the preceding paragraph, the Sierra de Nipe is mainly formed of two types of soils, the serpentine and limonite soils. The serpentine forming these soils, a metamorphic rock of eruptive origin, is a silicate of magnesium (H. Mg. Si. O_2), having a high content of MgO , possibly reaching 25 to 35 percent and a variable content of Al_2O_3 , FeO , NiO and Mn . Here follows an analysis of the serpentine of Sulphur Bank, according to E. S. Dana.

SiO_2	Al_2O_3	FeO	MgO	H_2O	NiO	Mn
39.62	1.59	7.76	37.13	13.81	0.33	0.12

Serpentine soils are represented in many countries, and they are clothed with typical vegetation correlated to local edaphic factors and known as serpentinophytes. These serpentinophytes like halophytes, calophytes, and zincophytes are chemomorphotic vegetation, represented by plants which, reacting to certain chemical elements found in the soil, may develop morphological changes. The serpentinophytes have been extensively studied by Novák, Sadebeck, Suza, Neger, Linstow, Schustler and Lämmermary. Among the investigators of this subject, we believe that F. Novák has given an excellent interpretation to this soil and its endemic flora. Novák believes that the serpentinophytes are controlled by the $\text{Mg}:\text{Ca}$ ratio, which must be in the soil with an excess of Mg ions. In Cuba, however, even though the serpentine soils cover a large part of the island, its vegetation has not been adequately studied. In another part of this paper, the possibility of existence of relict species in Sierra de Nipe has been mentioned, but there is no doubt that here also on this serpentine soil we are in the presence of a great center of neo-endemic or vicarious species being mainly selected by local edaphic phenomena.

The other important soil in Sierra de Nipe is the limonite, a hydrous ferric oxide ($2\text{FeO} \cdot 3\text{H}_2\text{O}$), which forms extensive mineral deposits from 1 to 6 m. in thickness. In the upper horizons, this soil is very red, dusty and permeable; graduating to yellow clay in the lowest horizons. In this ore, oxide of manganese and nickel are frequently present. The

content of manganese is about 13 to 26 percent which makes this ore of commercial value. The disadvantages of the ore's low quality is offset by the simplicity of obtaining the mineral, since it may be mined with steam shovels from the surface. At present a large plant is being constructed for the purpose not only of extracting the manganese, but also the nickel which this ore contains, even though it is only to 3 or 5 percent.

The concentration of these limonite deposits is due to decomposition of the serpentine by weathering, a phenomenon known as laterization. This process is made possible by the content of iron peroxide which is found in the serpentine and which is deposited as more or less pure hydrated iron oxide. The lateritic process is highly interesting in tropical regions, where the bacteria of the soil may destroy a large quantity of humus which would otherwise form there. Consequently the atmospheric agents may act directly upon the rocks, disintegrating the content of iron peroxide and depositing it in the soil as iron oxide, giving to these soils that red color so typical in tropical countries. In the case of the limonite soils of Sierra de Nipe, the almost complete absence of organic material is very characteristic and explains the high concentration of iron oxide, as well as the poor representation of fossils. Nevertheless, in the eastern part of the range, and near the headwater of Río Mayarí, are found interesting fossil deposits in a calcareous ferruginous substratum. This site was studied some years ago by the late Dr. A. Hollick, who collected a large number of specimens which are now in the collection of the New York Botanical Garden.

CLIMATE

Little is known about the climate in Sierra de Nipe, because no meteorological records exist. Nevertheless, in the short time that we remained in this region, we observed that its climate was similar to that of the rest of the mountainous regions of the oriental part of Cuba, with exception of the rainy season, which in this region is very peculiar. The precipitation during the year probably varies between 1,000-1,500 mm., of which the major amount falls during the rainy months, October to February, while March, April and July are the driest months of the year. This rainy season of the northeastern part of Cuba is an interesting phenomenon, because the winter months are generally the driest months of the year in Cuba. Temperature, as in all the mountainous regions of Cuba, is fresh and cool, but never reaches the freezing point. Predominant winds are from the northeast, including those which bring the rain. It is interesting that although the pine forests of Sierra de Nipe are only 600 m. above sea level, frequently a dense fog covers them, such as occurs in other mountainous parts of Cuba at elevations of 1,000-2,000 m. (Fig. 25).

INHABITANTS

The permanent population in the high regions of the Sierra de Nipe consist only of a few German families who established themselves there some years ago for lumbering. Farther to the south also there are some Cuban families who are engaged mainly in truck gardening and dairy farming on a very small scale. At present owing to the establishment of a large sawmill, and as well the presence of a company engaged in the exploitation of various minerals from the region, the population has considerably increased, but these people without doubt will leave the region as the work of these companies becomes restricted.

As we have above pointed out, the agriculture in this region is not of great importance, being mostly restricted to gardening for the purpose of supplying the needs of the families in this region. For the purpose of gardening, the soils to the south and southeast of Río Piloto are the most suitable, and here is where several Cuban families are engaged in this activity. Even though the agriculture is not extensive in this region, lands cleared in preparation for gardening frequently could be seen (Fig. 3). In certain sections of the upper part of Sierra de Nipe, we saw land which possibly at one time was pine land, but having been cleared out in part by lumbering and fire, has come to be covered by a thick grass community which is used for grazing (Fig. 11).



FIG. 3. View of a clearing in the forest made for agricultural purposes.

The style of the houses in this area is very interesting, bearing more resemblance to log cabins of the temperate climes than to the native "bohío" (Fig. 4). Nevertheless, the interior is that of the typical Cuban bohío, as is its roof, which is made of "guano" from the only two palms in the pine region, *Copernicia yarey* and *Coccothrinax yuraguana* var. *orientalis*. The general aspect of the house is more hygienic than that of the common bohío, and its floor and walls of pine is one of its most conspicuous advantages.

THE LUMBER INDUSTRY

The limonite soils of Sierra de Nipe are not only of importance to mineralogy but also to forestry,



FIG. 4. "Bohío." Notice the walls of pine logs.

since it is precisely on these soils of the Sierra that we find one of the most extensive pine forests of Cuba, composed of a single species, *Pinus cubensis*. Generally the tropical regions are not considered important in the timber production of pine or other Gymnosperms. Even in those tropical regions where pine is found, locally its exploitation does not receive great attention. As is widely known, lumbering in tropical regions is sporadic in character since most of the woody plants are found in isolated areas with rugged terrain. But here on the limonite soils of Sierra de Nipe, the pine lumbering is of immense value as we found large and pure stands of pine which permit their exploitation on an intensive scale.

Exploitation of the pine forest of Mayarí began many years ago with the establishment of a number of small sawmills in different localities. A turpentine industry also existed but was abandoned some years ago, and today one may still see some of the trees which were tapped. It is impossible for us to know just what these pine forests were like before their disturbance, but we believe that the number of trees per unit area was undoubtedly greater than today, as was their height and diameter, since exploitation inevitably removes the largest and tallest individuals. Pines which are cut today are 10-15 m. to the lowest branches, 20-25 m. in total height, and with a diameter of 30-40 cm. d.b.h. Larger individuals are rare, but nevertheless we have seen trees 30 m. high with diameter of 60 cm. d.b.h. The number of pine per unit area is difficult to determine, since the stands are highly variable and exploitation has completely altered normal conditions. On the best sites the distance between trees is about 4-6 m. with an average of 60-90 trees suitable for cutting for each 10,000 sq. m. These figures appear somewhat optimistic when one takes into consideration the pine forest in general. The total area covered with pine in the Sierra de Nipe is approximately 20,000 hectares, but some of them are in out of the way places and commercially impracticable to harvest.

Actual lumbering has been carried on by the Bahama Company, which has constructed in the pineland a large sawmill together with buildings, roads and

other necessary facilities. Among these roads, the largest is the "camino real," which extends from south of the mountains to the town of Antilla on the north coast, where are located the warehouses of the company. The logs, some 8-10 m. in length, as cut in the pine forest, are brought to the mills for milling. The capacity of the mill is fairly large and generally some 10,000 board feet are cut daily. To date some 9,000,000 board feet have been cut, and according to calculation, some 12,000,000 board feet still remain in accessible regions. In addition to the pine, certain other woods like *Swietenia mahagoni*, *Cedrela odorata*, *Podocarpus aristulata* and *Juniperus barbadensis* are frequently cut.

VEGETATION

ENDEMICISM IN THE FLORA OF CUBA

The flora of Cuba is well known for the high proportion of endemic species which are restricted mainly to a few regions of the island. Of the 45,570 square miles comprising this country, approximately one fifth is mountainous, and these are the major centers of endemism. The rest of the island, low and mainly covered with sabanas, has a fairly uniform flora. The majority of the plants that occur here are also frequent in other neo-tropical regions, including the Bahamas and Florida.

Of the mountainous regions of Cuba, only three areas deserve special mention because of their high degree of endemism: One of these is Sierra de los Organos, situated in the west part of the island. The others are the well-known Sierra Maestra in the southeast, and the mountainous region which extends from the Sierra de Nipe to Sierra de Moa in the northeastern part of Cuba.

Endemism of the Sierra de los Organos actually extends somewhat to the siliceous sabanas which surround it. The Sierra de los Organos is composed largely of a compact grayish-blue limestone of the upper Cretaceous. Owing to the kind and stage of weathering they have developed into a group of very typical isolated hills, which rise steeply out of level plains, and are known locally as "mogotes" because of their similarity to haystacks. Many of these mogotes have certain species endemic to a single hill, and many others are endemic to the whole Sierra: But in general the flora of these hills appears to have a slight relation to the vegetation of the mountainous regions of Central America. Such relationship is more striking in the flora of the sabanas surrounding these mogotes, where many plants occur which are native also to Honduras, Yucatan, and the southeastern United States.

In the eastern part of the island is the Sierra Maestra, one of the best known endemic areas in Cuba. Here the highest elevations of the island are found, including Pico Turquino, Palma Mocha, Loma Joaquín, Loma Regino, La Bayamesa, Loma del Gato, La Gran Piedra, La Perla, Monteverde, and many other famous botanical areas. These mountains, which in general are formed of igneous rocks and

surrounded by a frame of limestone at the base, possess a very dense cover of vegetation including the most extensive forests of Cuba. Endemism in these regions is well known, but the majority of these species are widely distributed within these mountain regions, and many others are related to species existing in other islands of the West Indies. In general the flora of the Sierra Maestra has a strong affinity with that of similar regions of the Antilles and northern South America.

The other center of endemism is to the north of Sierra Maestra, and consists of, from west to east, the Sierra de Nipe, Sierra de Cristal, Sierra de Moa and Cuchillas de Toa. These places comprise without doubt, the most important endemic centers of the entire island. Their flora, in general, develops a striking difference to the rest of the vegetation of Cuba and does not appear to have that great affinity which the flora of Cuba has with that of the rest of the Caribbean region. The number of endemic species described from this region, is greater than that of any other endemic center of the island; to these one must add a large number of endemic genera, as: *Svenhedinia* (Magnoliac.); *Tetralis* (Bixac.); *Shaferodendron* (Sapotac.); *Phidiasia*, *Dasytropis*, *Sapphoa* (Acanthac.); *Schmidtottia*, *Eosanthus*, *Acrosynanthus*, *Ariadne*, *Shaferocharis* (Rubiace.); *Tetraperone*, *Feddea*, *Koehneola*, *Harnackia*, *Ciceronia* (Compositae); and *Hemithrinax* (Palmar.).¹

THE "ANTILLEAN MONTANE FOREST"

The vegetation of Sierra de Nipe, like most of the mountainous vegetation of Cuba and the other West Indies islands, is generally referred to as rain forest, but it should be clearly recognized that it is not the same as the true "rain forest" (Haviland), which occurs in the extensive jungles of Tropical America and Africa, at low elevation, where the temperature is rather warm all through the year, with an annual precipitation of 2,000-4,000 mm. In Cuba, as in the rest of the Antilles, humid forests are found at elevations of 500-2,000 m., where temperature is quite cool and there is an annual precipitation of only 1,000-2,000 mm. This typical humid vegetation of the mountainous region of the Antilles is not only distinguished from the true rain forest by the geographic and climatic factors just mentioned, but also in its floristic composition. Here numerous plants are found which represent typical families of temperate climes. They are mainly *Pinaceae*, *Cupressaceae*, *Juglandaceae*, *Ericaceae*, *Vacciniaceae*, *Magnoliaceae*, *Berberidaceae*, *Rosaceae*, *Ulmaceae*, *Cornaceae*, *Clethraceae*, *Hydrophyllaceae*, *Oleaceae*, *Pirolaceae*, *Cunoniaceae* and *Brunelliaceae*.

Recently there have been several workers who have studied and attempted to establish a proper system of classification for the vegetation of the mountain region of the Antilles. Among these workers, F. Shreve, W. R. Barbour and J. C. Beard should be mentioned. The first mentioned author has written

¹ The *Hemithrinax ekmaniana* has been described from the Mogotes de Caguaguan, Sagua, Santa Clara; but we do not believe it belongs in this genus.

a valuable account of the mountain vegetation of Jamaica entitled "A Montane Rain Forest." However, this writer when discussing such vegetation unaccountably uses the term rain forest and never uses the term which his paper bears as its title. It is apparent that F. Shreve does not pretend to present the mountain vegetation of Jamaica as a climax formation or a sub-type of the "rain forest" (Haviland), nor is it his intention to propose a name for such vegetation.

Barbour in a recent work introduces a quite extensive nomenclature for this type of vegetation with corresponding translation into various languages spoken in the Western Hemisphere. For such vegetation he enlists names as "rain forest" (Haviland), "cloud forest" (Ruthven), "tropischen regengrüne Wälder" (Drude), "immergrünen Laubbäumen Wälder" (Drude), "Pluviisilvae" (Rübel), "immergrünen Laubwälder" (Warming), "tropischen immergrünen Regenwälder" (Drude), "tropischen Regenwälder" (Warming), and many other terms. However, there is not a clear definition as to how these are applied to the various vegetations.

Beard, recognizing the great need for a classification of this mountain vegetation of the West Indies, has written several interesting papers on this subject but unfortunately sometimes has freely used terms as "rain forest" (Haviland), "monsoon forest" (Schimper), and "elfin wood" (Schimper). Of these, the first has already been mentioned, and will be further discussed at the end of this section. The other two could be only applied safely to the old world. Beard, nevertheless, has a good understanding of the matter and his procedure on the classification of such vegetation, based mainly on Clements', is satisfactory, but the nomenclature which he uses does not seem to be entirely proper. For instance, this author discusses a vegetation under the name of rain forest and which he considers as a climax formation, but he adds that such vegetation does not occur in the Amazon basin. He discusses another vegetation of the mountains as a typical formation which he calls "montane rain forest"² (Shreve or Beard?), a term that could be used in the concept of Shreve, with some consideration, but not in the intrinsic concept of Beard.

It is not the purpose of this paper to establish a nomenclature or a system of classification for the vegetation of the West Indies. Nevertheless, we believe that in order to proceed in the classification of the vegetation of the mountainous regions of Cuba and the other West Indies and its nomenclature, a brief historical discussion of the matter should be attempted. Taking into consideration the opinions of classical workers as Grisebach, Drude, Schimper, Köppen, Warming, and Clements, we may divide the world vegetation into about ten great divisions or climaxes which may be, in turn, sub-divided into minor units of vegetation. To illustrate this matter,

² Beard says "the writer's use of 'montane' is not a synonym for 'mountain.'" We do not know what is meant by this, but believe that this term has been derived from the mountains where this vegetation is found.

we believe that the system of Köppen will be useful.² This author lists five preliminary great types of vegetation, one of which is the Megatherm (A. de Candolle). This is defined by the author as that vegetation found from 0° to 25° latitude, north and south, at an altitude from sea level to 1,500 m. (thus lowering in altitude in relation to the distance from the equator). There are two seasons, winter and summer, the annual rainfall is approximately 2,000 mm. with 60 mm. in the driest month which month is in the winter season. The temperature is uniformly warm oscillating only from 1° to 6° C., and the minimum temperature being 18° C.

The Megatherm, is itself divided in two climax formations, "Lianenklima" (Köppen), and "Baobabklima" (Köppen); the first being more or less equal to the real "rain forest" (Haviland), and the second to the sabana. The Lianenklima is found approximately between the 0° and 15° north and south latitudes, but running to the proper limits of the Megatherm in some places of the West Indies, Central America and the Malay Peninsula. The temperature and rain coincide with that of the Megatherm with slight differences. The Lianenklima is warmer and has more rain than the Baobabklima. The Lianenklima, with further study, will develop climatic sub-types, of which our mountain vegetation undoubtedly forms one. Further study of these major groups or climatic sub-types, will develop easily recognized minor units of vegetation and communities. It seems that Barbour and Beard have this in mind, but the difficulty which we see, is that both workers use a nomenclature which seems improper for such vegetation. Besides this, the constant use of "rain forest," "montane rain forest," and other terms with the noun "rain" makes the nomenclature of this vegetation confused.

For this reason, we propose the name "antillean montane forest" as a climatic sub-type of the "rain forest" (Haviland). Because of the lack of a complete knowledge of the mountainous vegetation, as well as the local climatological and edaphical factors of the whole West Indies, we cannot give a precise description and limit for the "antillean montane forest." Nevertheless, we believe that in general this vegetation is represented in those mountain regions of the West Indies where the average temperature is about 10° to 20° C., it being somewhat cooler in winter time but never reaching a freezing temperature. The annual rainfall may be around 2,000 mm., slightly more in a few localities. The altitudes where this vegetation is found must vary with different localities. In the Lesser Antilles, the "antillean montane forest," seems to be found from 800 m. to 1,000 m., but in the Larger Antilles, it may be found from 200 m. to 2,000 m. All this, undoubtedly, can be altered with the windward position of the land masses of those regions.

It would not be safe at present to include the vege-

² After this paper was written, the Trewartha book which extends the Köppen work came to my attention, and it is mentioned here for those readers who may be interested.

tation of the southeastern part of Central America in the "antillean montane forest," but with further study, it may be that the vegetation of the mountains of British Honduras and that of the mountains of the Atlantic shores of southern Central America, could be considered part of this vegetation.

VEGETATION OF SIERRA DE NIPE

The difficulty of describing a tropical plant community is well known, but it is more difficult to name them in terms of their dominants, for in reality true dominants do not exist. It is this fact which presents our first problem in describing the different communities of Sierra de Nipe. In spite of this fact, we refer here to a community which may be called "pinar," where the pine is the dominant arboreal element. Beside the pinar, we will mention seven other communities which at this time cannot be designated in terms of dominant or predominant species, and now we will list them by their vernacular names, such as "charrascal," "sabana," "sao" and "monte." To these we must add a hygrophilous community, the monte of the calcareous soils and the vegetation of the Mensura. In describing these communities, an attempt is made to list the plants in order of their predominance.

THE PINAR

Among all the communities of Sierra de Nipe, the most extensive is the pinar which occupies all the limonite soils between 400-600 m. elevation. This community attains its best expression on the central plateau where it is known as the "Pinar de Mayarí" (Fig. 24). Other pine regions are the "Pinar Colorado," to the west of La Mensura; the "Pinar San José" and the "Pinarito," both in the northwest of the Sierra.

Grasses and sedges represent the true dominant of the pinar: However, the pine holds an important position, at least as a physiognomic dominant and as a dominant of the arboreal canopy. The pinar is formed of a single species of pine, *Pinus cubensis*, which is 15-25 m. high and 30-40 cm. d.b.h. This tree is generally 4-10 m. apart and lightly branched (Figs. 1, 5, 6, 7 and 8). These factors make this pinar quite light in comparison with the same type of vegetation in temperate regions. The trunk of this pine is erect and slender, covered with a reddish thick-scaled bark. The leaves of dark green are in 2's and rarely in 3's, 4-15 cm. long and somewhat rigid. As mentioned previously, the original aspect of the pinar is difficult to imagine after long years of inappropriate exploitation, but undoubtedly the stand was much denser. There are a large number of different grasses and sedges which do not reach much more than 50 cm. high covering the soil of this pinar. Among these there is a group of small herbaceous plants of the same height as the grasses. We also find here a group of woody and more tropical shrubs as well as some plants from neighboring communities.



FIG. 5. The pinar community with the single arboreal element, *Pinus cubensis*.



FIG. 8. *Bactris cubensis* in right corner. Notice that this pine stand has been thinned by lumbering.

Among the grasses collected here are the following:

<i>Leptocoryphium lanatum</i>	<i>Lasiacis sloanei</i>
<i>Imperata brasiliensis</i>	<i>Panicum nitidum</i>
<i>Panicum aciculare</i>	<i>Paspalum saugeitii</i>
<i>Aristida refracta</i>	<i>Panicum chrysopsidifolium</i>
<i>Paspalum ruzestri</i>	<i>Lasiacis sorghoidea</i>
<i>Andropogon gracilis</i>	<i>Achlaena piptostachya</i>
<i>Andropogon semiberbis</i>	<i>Triscenia ovina</i>
<i>Arundinella confinis</i>	<i>Digitaria panicea</i>
<i>Panicum arenicoloides</i>	<i>Scutachne dura</i>
<i>Arthrostylidium urbanii</i>	<i>Panicum scoparium</i>
<i>Setaria subtransiens</i>	<i>Ichnanthus mayarensis</i>
<i>Cenchrus brownii</i>	<i>Ichnanthus nemorosus</i>
<i>Panicum wilmingttonense</i>	<i>Imperata contracta</i>
<i>Lithachne pauciflora</i>	<i>Panicum beyeri</i>
<i>Lithachne pineti</i>	<i>Setaria tenax</i>
<i>Lasiacis rugelii</i>	<i>Andropogon leucostachyus</i>

The following sedges are found in this community:

<i>Rhynchospora boringuensis</i>	<i>Rhynchospora tenuis</i>
<i>Rhynchospora ceruna</i>	<i>Scleria stereorrhiza</i>
<i>Rhynchospora deflexa</i>	<i>Scleria pilosa</i>
<i>Rhynchospora crispata</i>	<i>Bulbostylis papillosa</i>
<i>Rhynchospora nipensis</i>	<i>Bulbostylis vestita</i>
<i>Rhynchospora scabrata</i>	<i>Bulbostylis subaphylla</i>

Among the small herbaceous plants which occur here, are the following:

<i>Phyllanthus micranthus</i>	<i>Desmodium barbata</i>
<i>Polygala paniculata</i>	<i>Nevrolaena lobata</i>
<i>Chaptalia dentata</i>	<i>Emilia rondifolia</i>
<i>Emilia sonchifolia</i>	<i>Melochia nipensis</i>
<i>Tubiflora shaferei</i>	<i>Bidens ekmanii</i>
<i>Vernonia angustissima</i>	<i>Chaptalia nipensis</i>
<i>Muntingia calabura</i>	<i>Galactia revoluta</i> (climber)

Here also we find a group of herbaceous plants which are larger than the preceding and sometimes quite woody, among these the following are frequent:

<i>Psychotria graminifolia</i>	<i>Callicarpa nipensis</i>
<i>Psychotria subulata</i>	<i>Neobraccia valenzuelana</i>
<i>Senecio shaferei</i>	<i>Pictetia marginata</i>
<i>Eupatorium iacifolium</i>	<i>Chaptalia leptophylla</i>
<i>Mikania reticulosa</i>	<i>Chaptalia crassiuscula</i>
<i>Acrocyanthus paraiso</i>	<i>Buchnera elongata</i>
<i>Cestrum pinetorum</i>	<i>Baccharis scoparioides</i>
<i>Brunfelsia shaferei</i>	<i>Baccharis shaferei</i>
<i>Mitracarpum linearifolium</i>	<i>Pachyanthus reticulatus</i>
<i>Banisteriopsis pauciflora</i>	

In the preceding description, the reader should note how a group of grasses, sedges and other herbaceous plants cover the ground of the pinar, forming a community commonly believed to be typical only of

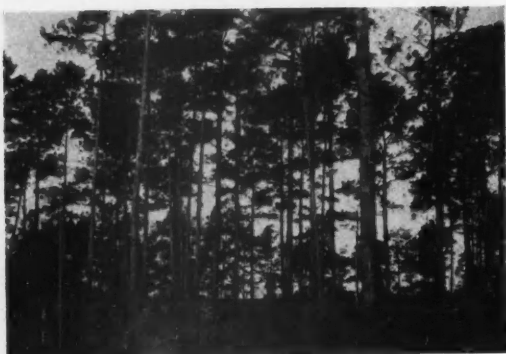


FIG. 6. A thick stand of *Pinus cubensis* with grasses and sedges covering the soil.



FIG. 7. *Coccothrinax yuraguana* var. *orientalis* growing under the *Pinus cubensis*. Notice the extensive and undulating limonite soils.

temperate regions, but found actually in various parts of Central America and the Antilles. On the other hand, if one observes the margins of the pine forest, and the transition between this community and the monte, one finds a group of larger and woody shrubs, typical of tropical vegetation, such as *Tabebuia pulverulenta*, *Pithecolobium pinetorum*, *Mettenia globosa* and *Eugenia nipensis*, all from 2-4 m. in height. Two other shrubs frequent in this community are: *Xolisma myrsinefolia* with white flowers and *X. obtusa* with yellow flowers.

The most interesting occurrence in this community, is the frequent groups of plants or colonies of a single species, a thing not so common in tropical regions. Among such colonies a principal one is formed by *Euphorbia nipensis*⁴ (Fig. 9), a small shrub 50-60 cm. high, woody, slightly branched, erect, and with lanceolate leaves about 5 cm. long. The inflorescence bears bracts of bright red color, about 3 cm. long and as decorative as that of the exotic *Euphorbia pulcherrima*.

Other pure colonies that are found in the pinar, are those formed by *Casearia aquifolia*, an attractive plant about 30 cm. high, covered with beautiful pale pink flowers and with small and very spiny leaves (Fig. 10); *Clerodendron nipensis* 1 m. high, erect, slightly branched and with attractive white flowers



FIG. 9. A pure colony formed by *Euphorbia nipensis* in the pine land.

⁴ We present here this new combination because of the importance of that species in this community: *Euphorbia nipensis* comb. nov. Carabía.—*Euphorbiadendrum shafteri* Millsp., Field Mus. Bot. Publ. 2(9): 373. 1913. (Not *Euphorbia shafteri* Dinter in Fedde., Repert. 17: 304. 1921.)

Euphorbia nipensis and *E. podocarpifolia*, both endemic of Sierra de Nipe, belong to a group of Euphorbias represented by about a dozen species common to the Antilles, Mexico, Peru, and Colombia. All those Euphorbias represent without any doubt a homogenous group, which is easily distinguished by their large and showy bracts. But this character or any other does not permit separating it from Euphorbia. Nevertheless on two occasions new genera have been proposed for this group; first the genus *Adenorima* Rafin., and later *Euphorbiadendrum* Millsp.



FIG. 10. Close up of *Casearia aquifolia* in the pine land.

4-5 cm. in length; *Guettarda ferruginea*, a small shrub 1-2 m. high, branched, with coriaceous leaves of a ferruginous color and with white flowers; *Vaccinium cubense*, 1 m. high, with small coriaceous leaves and with numerous flowers that are pink or red outside and white inside.

At times plants are found in the pinar which typically do not belong to this community, but which are characteristic of the charraseal, sabana or other contiguous communities. As an example we may mention *Agave shafteri*, a plant of the charraseal but also seen occasionally in the pinar. Frequently a palm, *Coccothrinax yuraguana* var. *orientalis*, forms large colonies within both the pinar and the sabana, but which is actually typical of the latter community (Fig. 7). Another palm typical of the margins of brooks and ravines, *Bactris cubensis*, appears in humid sites of the pinar (Fig. 8).

THE SABANA

This community actually covers large areas of open land with soil varying from almost pure limonite to rocky serpentine soil. Much of this community may be considered as true sabana, but possibly in some cases where the soil is limonite, it was pine land,



FIG. 11. Open sabana covered with *Imperata brasiliensis* and *Leptocoryphium lanatum*.



FIG. 12. A view of the sabana with *Copernicia yarey* and *Coccothrinax yuraguana* var. *orientalis*. Some shrubs of the charrascal may be seen also here. This picture taken from east to west shows the back of the calcareous cliffs at Cayo del Rey and the extensive plain to the west of the Sierra.

where lumbering and fire have destroyed completely the pine and the shrubby vegetation (Fig. 11). In other places where the soil is rocky serpentine, we found a conspicuous number of shrubs typical of the charrascal (Fig. 12). Nevertheless that many of them are sabanas is confirmed by the presence of the palm, *Copernicia yarey* (Fig. 12), a genus typical of those communities. In the sabana, we frequently find two palms, the already mentioned, *Copernicia yarey*, which is 4-6 m. high, having leaves of the fan type and large hanging inflorescences. The other palm is *Coccothrinax yuraguana* var. *orientalis*, which is 2-4 m. high with very slender trunk covered by the base of the petioles, and also having fan-shaped leaves. Much of the soil of the sabana is covered by a group of grasses and sedges, the majority of which are the same species found in the pinar; however, *Imperata brasiliensis* and *Leptocoryphium lanatum* predominate (Fig. 11). In some cases these grasses give way completely to a fern *Pteridium aquilinum* var. *caudatum*, which forms dense stands 5-10 dm. high and under which is sometimes found *Zamia pumila* (Fig. 13).



FIG. 13. Slope of the sabana covered with *Pteridium aquilinum* var. *caudatum*.

THE CHARRASCAL

This is the name employed in this locality for a semi-xerophytic community, formed mainly of woody shrubs and small trees 6 m. high or less, with stems 5-10 cm. in diameter. The leaves are generally small and coriaceous, revolute, smooth and lustrous on the upper part and with tomentum on the under surface. Among the most common type of leaf is that varying from elliptic to oblong, about 5 cm. long, 1-2 cm. wide and with very short petioles. Another common leaf type is long, narrow, pointed or spiny, and more or less perpendicular in relation to the stems. Among the tall shrubs or trees which form the upper layer of this community, are some having a typical terminal rosette of leaves that makes them very conspicuous.

The charrascal in respect to the area it occupies is second to the pinar. However, from a floristic point of view, this community is the most interesting of Sierra de Nipe, being complex in its composition and very rich in endemic species. The charrascal is a vegetation that presents a purely local, edaphically controlled phenomenon, being correlated to different rocky serpentine soils, which vary from raw rocky serpentine to limonite soil. In this form, variation of charrascal can be observed through broad ecotones, making a classification of different types of charrascal difficult. Nevertheless, two charrascal types may be recognized. The first is fairly open vegetation, formed of a limited number of small shrubs, and found on the very rocky soils (Figs. 14 and 15). The second type of charrascal is more widely distributed, more dense and formed of a large number of shrubs and small trees (Fig. 16).

The open charrascal may be named, according to its predominant species, "Plumeria-Spathelia-Euphorbia." The species themselves are *Plumeria nipensis* (*P. obtusa*),⁵ *Spathelia vernicosa*, both 4-5 m. high, and *Euphorbia podocarpifolia*, 1 m. high. In the same manner the dense charrascal may be named "Euphorbia-Spathelia-Metopium," due to the pre-



FIG. 14. A marginal view of the open charrascal with *Plumeria nipensis* and *Agave shawii* shown at the right corner. In the background the back of the calcareous cliffs at Cayo del Rey, and the extensive plain to the west of the Sierra may be seen.

⁵ Woodson, R. E. North American Flora 29(2): 117. 1938.



FIG. 15. *Agave shaferi* with some shrubs of the open charrascal in the background. To the left *Coccothrinax yuraguana* var. *orientalis*. The ground is covered by *Arthrostyidium capillifolium*.

dominance of *Euphorbia podocarpifolia*, which in this community reaches a height of 4-6 m., and *Spathelia vernicosa* and *Metopium venosum*, both 4-5 m. in height.

In the *Plumeria-Spathelia-Euphorbia*, the predominant species of the upper layer is *Plumeria nipensis*, a sparingly branched tree with fleshy twigs 3-4 cm. in diameter, and with numerous lanceolate leaves forming a rosette at the apex of the stems (Fig. 14). Second in importance is *Spathelia vernicosa*, slightly branched, with 10-20 leaves forming terminal rosettes, from which arise large and very showy inflorescences. The third predominant shrub is *Euphorbia podocarpifolia*, highly branched and covered with small linear leaves which give it a dense appearance (Fig. 17). Among other shrubs of the upper layer are, *Phyllanthus cinctus*, 3-5 m. high, slightly branched, with flowers of 2-3 cm. in diameter; *Rheedia ruscifolia*, occasionally a predominant, 3-5 m. high, with numerous spreading branches, and small coriaceous spiny leaves. The upper layer of this community is filled with the following additional plants:

Belairia spinosa
Dodonaea jamaicensis
Drypetes mucronata

Byrsonima spicata
Pera polylepis
Rondeletia stellata



FIG. 16. A marginal view of the thick charrascal. In the foreground *Euphorbia podocarpifolia*.



FIG. 17. *Euphorbia podocarpifolia* in the open charrascal.

In the lower layer of this community, the most conspicuous plants are *Euphorbia podocarpifolia* and *Agave shaferi* (Fig. 15). In addition the following plants complete the lower layer:

Eugenia pinetorum
Anastrophia cubensis
Croton monogynus
Croton bispinosus
Coccoloba woodfredensis

Leucroton saxicola
Calycogonium rosmarinifolium
Jacquinia robusta
Acidocroton pilosulus
Arthrostyidium capillifolium

The *Euphorbia-Spathelia-Metopium* charrascal is so dense, it is difficult to recognize distinctive layers. Nevertheless we may consider two groups of plants. In the first group forming the upper layer, the predominants are *Euphorbia podocarpifolia*, which here reaches a height of 4-6 m. (Fig. 16); *Spathelia vernicosa*, mentioned previously; and *Metopium venosum*, a slightly branched shrub 3-4 m. high, with a terminal rosette of leaves. In this community certain other plants may become predominant, taking the place of the other mentioned species; such are: *Purdiea cubensis*, *Spathelia cubensis* and *Belairia arborea*. Other shrubs or small trees in the upper layer are:

<i>Erythroxylum coriaceum</i>	<i>Erythroxylum rotundifolium</i>
<i>Periqueta cubensis</i>	<i>Elaphrium glaucum</i>
<i>Casearia arborea</i>	<i>Alvaradoa arborescens</i>
<i>Chrysophyllum oliviforme</i>	<i>Belairia cubensis</i>
<i>Cassia nigricans</i>	<i>Savia longipes</i>
<i>Cotema spiralis</i>	<i>Antirrhoea shaferei</i>
<i>Harpalyce nipensis</i>	<i>Myrris lineata</i>
<i>Eugenia flavicans</i>	<i>Helietta glauca</i>

The other group of shrubs of this community, generally 1-3 m. high, is represented by:

<i>Purdiea stenopetala</i>	<i>Rheedia marginata</i>
<i>Antirrhoea abbreviata</i>	<i>Eugenia fadyenii</i>
<i>Exostemma myrtifolium</i>	<i>Eugenia aeruginosa</i>
<i>Gymnanthes albicans</i>	<i>Shaferodendron mayarensis</i>
<i>Guettarda ferruginea</i>	<i>Coccoloba coriacea</i>
<i>Guettarda monocarpa</i>	<i>Lippia alba</i>
<i>Phyllanthus pachystylus</i>	<i>Lantana trifolia</i>
<i>Guettarda valenzuelana</i>	<i>Pera pallidifolia</i>
<i>Schmidtottia cubensis</i>	<i>Senecio rivalis</i>
<i>Rondeletia nipensis</i>	<i>Senecio ericarpus</i>

On the margins of the charrascal, and in open sites, there appear small groups of shrubs only 0.5-1 m. high, such as *Coccoloba nipensis*, with revolute and very coriaceous leaves and a large and showy red inflorescence; *Croton bispinosus*, with small and rust-colored leaves and covered with long spines; *Baccharis shaferei* and *Harnackia shaferei*, both with very small leaves which are covered with an oily resin; *Portlandia brachycarpa*, with coriaceous and spiny leaves, and attractive large white flowers. Additional shrubs typical of the most open spaces and margins of this charrascal are:

<i>Helicteres trapezopholia</i>	<i>Eupatorium hypoleucum</i>
<i>Anona sclerophylla</i>	<i>Hedyosmum nutans</i>
<i>Anaethaphia shaferei</i>	<i>Senecio trichotomus</i>
<i>Borreria spinosa</i>	<i>Croton monogynus</i>
<i>Malgiphia horrida</i>	<i>Gonzalagunia brachyantha</i>

Between these shrubs and completely covering the soil, frequently is found a grass, *Arthrotylidium capillifolium*, and also the interesting *Mimosa ekmanii*. Sometimes between charrascals, it is interesting to see large open spaces where shrubs of a single species are predominant, one of these being *Bourreria pauciflora*, about 30-50 cm. high, with small coriaceous revolute leaves and small white flowers. Other of these colonies are formed by *Cordia pedunculosa*, having attractive white flowers, and by *Calycogonium rosmarinifolium*, 50 cm. high and having also small coriaceous leaves.

It is not rare to find in the charrascal several elements of the neighboring communities, among which the most common are the two palms of the

sabana, *Copernicia yarey* and *Coccothrinax yuraguana* var. *orientalis*.

As indicated previously, the charrascals extend to the margins of brooks and rivers, and, consequently, their floristic elements change significantly. Here we find certain small trees 2-4 m. high and smaller shrubs, with large dark green leaves, somewhat leathery, forming a thick stand. This new type of charrascal may be designated as "Byrsonima-Tabebuia-Rondeletia," due to its predominant elements: *Byrsonima crassifolia*, *Tabebuia inaequipes* and *Rondeletia stellana*, all of them about 3-4 m. high. The upper layer of this community is formed by the three mentioned predominants and the following small trees:

<i>Guettarda monocarpa</i>	<i>Savia cuneifolia</i>
<i>Ocasia nigrescens</i>	<i>Tapura orbicularis</i>
<i>Pithecolobium asplenifolium</i>	<i>Buxus rheidioides</i>
<i>Pithecolobium nipensis</i>	<i>Buxus olivacea</i>
<i>Tabebuia nipensis</i>	<i>Antirrhoea tenuiflora</i>
<i>Curatella striata</i>	<i>Tetralia nipensis</i>
<i>Bignonia nipensis</i>	<i>Acrocyanthus parvifolius</i>
<i>Ariadne shaferei</i>	<i>Phyllanthus punctulatus</i>
<i>Ariadne ekmanii</i>	

Other shrubs, smaller than the above mentioned, are:

<i>Amyris balsamifera</i>	<i>Psidium versicolor</i>
<i>Pilocarpus racemosus</i>	<i>Neobracea valenzuelana</i>
<i>Tabebuia potanophylla</i>	<i>Calyptanthus punctulata</i>
<i>Tabebuia picotensis</i>	<i>Tabebuia pulcherrima</i>
<i>Amyris stromatophylla</i>	<i>Tabebuia nigripes</i>
<i>Harpalyce nipensis</i>	<i>Ravenia simplicifolia</i>
<i>Eugenia monticola</i>	<i>Cassia shaferei</i>
<i>Eugenia flavicans</i>	<i>Coccoloba costata</i>
<i>Eugenia glabrata</i>	<i>Psychotria odorata</i>
<i>Calyptanthus chytaculua</i>	<i>Portlandia brachycarpa</i>
<i>Calyptanthus zuzigium</i>	<i>Portlandia polyneura</i>
<i>Brunfelsia linearis</i>	<i>Phyllanthus ellipticus</i>
<i>Cyrilla nipensis</i>	<i>Calyptanthus rotundata</i>
<i>Psidium guineense</i>	<i>Calyptanthus polysticta</i>
<i>Rondeletia subglabra</i>	<i>Pera longipes</i>
<i>Buxus pilosula</i>	<i>Purdiea microphylla</i>
<i>Exostemma longiflorum</i>	<i>Acidocroton pilosulus</i>
<i>Rondeletia lindeniensis</i>	<i>Lobelia oxyphylla</i>
<i>Chimarrhis cymosa</i>	<i>Protium fragrans</i>
<i>Exostemma barbatum</i>	<i>Buxus aneura</i>
<i>Pera ekmanii</i>	

Growing on some of the above listed plants, we find the following parasites: *Dendrophthora moniliformis*, *D. picotensis* and *D. pachycladia*.

A group of small herbaceous plants found in this community, are:

<i>Ascyrum hypericoides</i>	<i>Anaethaphia shaferei</i>
<i>Vernonia hieracioides</i>	<i>Anaethaphia oblongifolia</i>
<i>Vernonia leptocladia</i>	<i>Leucroton angustifolius</i>
<i>Vernonia urbaniana</i>	<i>Polygala oblongata</i>
<i>Neuroleuca lobata</i>	<i>Crotalaria quinquefolia</i>
<i>Senecio subquarrosus</i>	<i>Desmodium barbatum</i>
<i>Eupatorium ayapanoides</i>	<i>Galactia rudolphoides</i>
<i>Jatropha minor</i>	<i>Senecio plumbeus</i>
<i>Baccharis nipensis</i>	<i>Walleria laurifolia</i>
<i>Eupatorium shaferei</i>	<i>Croton repens</i>
<i>Phyllanthus apiculatus</i>	
<i>Exostemma purpureum</i>	

Among these plants, we find also certain grasses and sedges, among which the most frequent are:

<i>Panicum scoparium</i>	<i>Eleocharis flavescens</i>
<i>Arthrotylidium ambriatum</i>	<i>Eleocharis sintenisii</i>
<i>Aristida curtifolia</i>	<i>Dichromena radicans</i>
<i>Panicum beyeri</i>	<i>Scleria pilosa</i>
<i>Octadesmia oligophylla</i>	<i>Rhynchospora pruvionis</i>
<i>Rhynchospora cubensis</i>	<i>Rhynchospora shaferei</i>

HYGROPHILOUS COMMUNITY

All along brooks and rivers, we may find a vegetation more or less typical of those streams. In the upper watershed, however, where the streams cross along sabanas and charrascales, the vegetation is that of the community which is cut by the streams (Figs. 18 and 19). In these sites we may frequently see some plants as: *Copernicia yarey*, *Coccothrinax yuraguana* var. *orientalis*, *Plumeria nipensis*, *Rondeletia stellana* and *Agave shoferi*. Covering the soil on the same sites, frequently we find a grass, *Arthrostylidium capillifolium*.



FIG. 18. Brook running through open charrascale and the sabana. The small trees are *Rondeletia stellana*. To the right is *Plumeria nipensis*. In the background *Copernicia yarey* and *Coccothrinax yuraguana* var. *orientalis* may be seen.

The typical hygrophilous community is that which we find only along brooks and rivers and is under the direct influence of local moisture. Here we find sometimes a very luxuriant vegetation, formed by a large number of ferns, bromelias, lianas and other epiphytes. Much of this vegetation is covered with a dense canopy of large trees, which in many places have their trunks covered by mosses and small epiphytic orchids. In other places along rivers we may find another community not so luxuriant as the above mentioned, but always typified by groups of ferns, bromelias and small herbaceous plants. In this form, we may recognize various groups in this hydric vegetation, but at the end all of them intergrade through gradual ecotone.

In the upper part of the Sierra, we find along brooks and rivers a somewhat sparse community, in which three small trees are frequent; these are: *Alsophila aquilina*, a very spiny tree fern, 3-4 m. high; *Cassia shoferi*, a small tree 3-4 m. high, very branched; and *Hibiscus nipensis*, a spiny plant 2-3 m. high, with branching woody stems. Under these plants we often find a typical group of small *Phyllanthus* (Orbicularia), among which the most frequent species is *Phyllanthus scopulorum*.⁶ Grasses, sedges

⁶ This species belong to a very typical group of *Phyllanthus*, including plants 5-10 dm. high, fully branched and covered with small circular leaves. These plants occur in shady humid sites, and their distribution is limited to the mountainous eastern



FIG. 19. Vegetation alongside a brook of the upper part of the Sierra, where *Agave shoferi*, *Plumeria nipensis* and *Arthrostylidium capillifolium* can be seen.

and other small herbaceous plants found in this community are:

<i>Panicum scoparium</i>	<i>Eleocharis alveolata</i>
<i>Panicum zalapense</i>	<i>Hypericum fasciculatum</i>
<i>Eleocharis caribaea</i>	<i>Ascyrum macrosepalum</i>
<i>Eleocharis shoferi</i>	<i>Polygala paniculata</i>
<i>Eleocharis pachycarpa</i>	

Also here we find two terrestrial orchids, *Lycaste barringtoniae* and *Phajus tankervillei*.

Farther downstream, the rivers may flow through rocky areas and deep ravines and the vegetation becomes more luxuriant. In this new community the trees are 10-20 m. high, and form a thick stand through which little light penetrates. Here three

region of Cuba, with the exception of one or two widely ranging species. In recognition of the close relationship of these species, and in order to express their unity as a natural group, N. L. Britton established the genus *Orbicularia*. Detailed studies, however, show that it is not possible satisfactorily to separate these plants from the genus *Phyllanthus*. Nevertheless the following species could easily constitute the section *Orbicularia*: *Phyllanthus orbicularia*, *P. myrtilloides*, *P. shoferi*, *P. phlebocarpus*, *P. scopulorum*, *P. nordii*, *P. spathulifolius*, *P. estrellensis*, *P. cristallensis*, *P. breviramis*, *P. javelata*, *P. melanodiscus*, *P. apiculatus*, *P. baracoensis*, *P. cordiophyllus*, *P. coelophyllus* and *P. formosus*. The last named species was placed by Britton under a new genus, *Dimorphocladium*.

Another interesting group of *Phyllanthus* limited to the north-eastern part of Cuba, comprises the following species: *Phyllanthus cinctus*, *P. ovalifolius*, *P. pachystylus*, *P. punctulatus* and *P. brevistipulus*, all of which form a natural group which may constitute another section of the genus *Phyllanthus*.

tree species are found which are predominant in the upper canopy, and from which the community may be named "Jacaranda-Tabebuia-Cecropia." The three species are, *Jacaranda arborea*, a very attractive tree with blue flowers; *Tabebuia pachyphylla*, also with very attractive flowers and *Cecropia peltata*, a widespread plant (Fig. 20). Other tree species of the upper canopy are:

Linciera lingustrina
Sapium jamaicense
Didymopanax morototoni
Erythroxylum coriaceum
Colubrina ferruginosa
Petesioidea laurifolium

Buchenavia capitata
Calophyllum antillanum
Tapura orbicularis
Hirtella mollissima
Chione cubensis
Dipholia jubilla



FIG. 20. Mingled with *Tabebuia pachyphylla* and *Jacaranda arborea* is found *Cecropia peltata*, with white leaves. The pine is so conspicuous because this picture was taken from the top of the pine land. In the center can be seen the upper part of Salto del Sojo.

Under this canopy we find other smaller trees of different sizes, among which are the following species:

Acrotyanthus varifolius
Rauwolfia salicifolia
Ravenia simplicifolia
Gonzalagunia brachyantha
Piper stamineum
Ariadne shaferei
Cateebaea grayii
Cateebaea holacantha
Exostemma stenophyllum
Pithecolobium asplenifolium
Sapium cubense

Miconia cerasifera
Casasia nigrescens
Casasia shaferei
Psychotria pubescens
Psychotria costivenia
Exostemma purpureum
Trichilia trachyantha
Pithecolobium nipense
Cyrilla nipensis
Exostemma barbatum
Exostemma ellipticum

Lobelia oxyphylla
Rondeletia nipensis
Antirrhoea abbreviata
Eugenia viti-idaea

Svenhedinia minor
Calyptanthus rotundata
Calyptanthus rupicola

Here we find some interesting vines and creeper plants, such as:

Columnnea cubensis
Bignonia cubensis
Passiflora foetida var.
quinqueloba
Passiflora stenoloba
Passiflora nipensis

Rhynchosia nipensis
Passiflora rubra
Kajania ovata
Hydrocotyle oligantha
Galactia rudoiphoides
Galactia revoluta

On exposed sites of this community, we find certain smaller plants as well as a group of herbaceous ones, such as:

Wedelia ehrenbergii
Brunfelsia shaferei
Ciceronia chaptalioides
Chaptalia leptophylla
Chaptalia nipensis
Chaptalia crassiuscula
Chaptalia dentata

Ascyrum macrosepalum
Senecio plumbeus
Anastrophia oblongifolia
Borreria spinosa
Xolisma macrophylla
Gnaphalium domingense

The following grasses occur here: *Aristida curti-foia*, *Triscenia ovina*, *Panicum scoparium* and *Lithacne pineti*. Also here we find a few orchids, as: *Psilochilus macrophyllus*, a terrestrial, and two epiphytics, *Epidendrum acutifolia* and *Hexisea reflexa*.

In many places of the lower part of the Sierra the currents of the streams are slow, and alluvium is actively deposited on the margins. The arboreal vegetation on such sites is composed of species already mentioned, although differences in growth and abundance reflect the hydric condition. Under this thick canopy of trees, we find frequently some arborescent ferns as: *Alsophila aquilina* and *Cyathea arborea*, which form conspicuous colonies. Here and there, are large groups formed by a very spiny palm, *Bactris cubensis*, 3-4 m. high; and the interesting *Equisetum giganteum*, which is 3-4 m. high, with stems 2 cm. in diameter at the base. Over rocks and fallen trees are seen: *Pteris grandifolia*, *Psilotum nudum*, *Lycopodium fasiforme* and *Vriesia sanguinolenta*.

At certain stations are found very dense thickets of ferns, *Urticaceae*, *Piperaceae*, *Begoniaceae* and some other herbaceous plants as:

Dryopteris latens
Dryopteris efusa
Dennstaedtia rubiginosa
Dryopteris reptans
Asplenium dentatum
Polystichum decoratum
Aneimia nipensis
Dryopteris lonchodes
Adiantopsis radiata
Pilea microphylla
Pilea heteronema
Pilea repens
Pilea nipensis
Tragia volubilis

Peperomia scandens
Peperomia leoclemerocana
Peperomia carlo-wrightii
Peperomia comulata
Peperomia cubana
Peperomia hirta
Peperomia oblanceolata
Peperomia petiolaris
Peperomia subrotundiflora
Begonia wrightiana
Vernonia wrightii
Koehneola repens
Croton postratum

Near to the base of the southeastern part of Sierra de Nipe, the streams are slow flowing and run over calcareous rocks. The vegetation along them is significantly different from that described above. Here one single species may form large colonies. Among these colonies, one of the most frequent is formed by a palm, *Calyptronoma dulcis*. Other of these colonies are formed by *Calophyllum antillanum*; *Piper*

FIG. 21. *Piper scabrum* along the Piloto River.

scabrum, a tree 5-7 m. high (Fig. 21); *Miconia dodecandra*, a small tree with conspicuous inflorescences; *Carapa guinensis*, frequently seen along the Mayarí River; *Bucida buceras*, *Cecropia peltata* and *Didymopanax morototoni*.

MONTE

This community covers a considerable part of the Sierra de Nipe, and it is found almost from the base of the Sierra to about 1,000 m. of elevation. Nevertheless, in this section of the paper, we will discuss only that part of the monte found from about 200 m. to 600 m. of altitude. In other sections of this paper, we will describe the monte at the base of the Sierra de Nipe as well as the monte from 600 m. to 1,000 m. of elevation.

The monte here discussed is that found all around the Sierra, wherever the ground is not too steep and where soil is deposited, enough to support a typical wet forest. In most of the terrain around the plateau of Pinar de Mayarí, and from 400 m. to 600 m. we find a very good belt of monte. In the west side of the Sierra, the monte never takes the proportion that it does to the east, where we find monte from 600 m. to almost the base of the Sierra. Nevertheless, the most extensive monte, is that found to the south and southeast of the Sierra.

The monte is a community formed by a large number of trees, growing so close to each other that only a small amount of light can get through (Fig. 22). The tallest trees are about 20-30 m. high, and form a dense canopy, under which we do not find any particular layer, but a large number of smaller trees of different sizes. The trunks of most of these trees are quite smooth and slender, with a diameter of 20-90 cm. d.b.h., and some of them forming the typical buttress at the base. The leaves of the majority of these trees are simple, mesophyll, and many of them have a somewhat leathery texture. Under this vegetation it is not usual to find shrubs or any herbaceous vegetation, but, nevertheless in some open spaces a few shrubs may be found. In the clearer places of the monte, we also find some epiphytes (Figs. 22 and 23).

FIG. 22. A side view of the monte. *Guzmania monostachya* at the left.FIG. 23. *Vriesia wrightii*, on an open side of the monte.

The upper canopy of the monte is formed by the following tree species:

Nectandra coriacea
Calyptranthes suzygium
Calophyllum antillanum
Guarea trichilioides
Cotema woodfordensis
Tabebuia shaweri
Tabebuia pachyphylla
Reynosia wrightii

Juniperus barbadensis
Podocarpus aristulatus
Drypetes lateriflora
Chione cubensis
Cedrela odorata
Krugiodendron ferrum
Pera bumeiaefolia
Swietenia mahagoni



FIG. 24. Loma La Mensura rising from the plateau of Pinar de Mayarí.

Hieronyma nipensis
Chinarrhis cymosa
Fera ekmanii
Buchenavia capitata
Byrsonima spicata
Gymnanthes lucida
Zizyphus rhodoxylen

Andira jamaicensis
Muricea albescent
Sapium jamaicense
Clusia tetrastigma
Dipholis cubensis
Ocotea wrightii

Among the smaller tree species in this community, are the following:

Wallenia lauriflora
Exostemma caribaeus
Schoepfia chrysophylloides
Ouatea affinis
Sapium cubense
Prockia crusa
Drypetes mucronata
Behaimia cubensis
Rondeletia canellaeifolia
Guettarda monocarpa
Ximenia americana
Linociera ligustrina
Catalpa denticulata

Hyperbaena domingensis
Gilbertia arborea
Palicourea barbinervia
Linociera domingensis
Ilex macfadynii
Ilex clementis
Cassia shaferei
Pseudocarpidium rigens
Ouatea striata
Tapura cubensis
Dasytropis fragilis
Buxus retusa
Tocoyena cubensis

Among the few shrubs, which we find in this community, are:

Turpina paniculata
Ossaea nipensis
Geaneria nipensis
Vernonia menthaefolia
Vernonia densiliens
Eupatorium macrophyllum
Eupatorium polystichum
Xolisma obtusa
Eupatorium rhexioides

Gnaphalium indicum
Psychotria subulata
Senecio shaferei
Palicourea toensis
Psychotria graminifolia
Psychotria pubescens
Rondeletia alaternoides
Phyllanthus pachystylus
Brunfelsia shaferei

On certain open sites these shrubs are entirely replaced by a single species, *Solanum jamaicensis*, which is about 60 cm. high, profusely branched and covered with spines, forming thickets through which one cannot pass without extreme difficulty.

Lianas, creepers, epiphytes and parasites occasionally occur, among the more important of which are: *Cissus subavenia*, *Cissampelos pareira*, *Teramnus volubilis*, *Rajania ovata*, *Vitis tiliacifolia*, *Cissus microcarpa*, *Tontanea repens*, *T. pleuropoda*, *Rajania wrightii* and *Mucuna urens*. Among the epiphytes, are *Vriesia wrightii*, which sometimes covers trees from top to bottom (Fig. 23); *Tillandsia rubra*, 1-2 m. high; *Guzmania monostachya* (Fig. 22); *Catopsis floribunda* and *C. sessiliflora*. Of the parasites,

Dendrophthora buxifolia, *D. cubensis* and *D. picotensis* should be mentioned. Orchids though not numerous in this monte, are nevertheless represented by a large number of species, such as:

Encyclia oncioides
Polystachya luteola
Epidendrum cochleatum
Epidendrum replicatum
Epidendrum neoporpax
Pleurothallis corniculata
Brassia caudata
Epidendrum jamaicense
Epidendrum rivulare
Dichaea hystrixina

Lepanthes melanocaulon
Lepanthes prietidia
Lepanthes lindmaniana
Pleurothallis shaferei
Pleurothallis sertularioides
Stelis ophioglossoides
Stelis ekmanii
Polystachya foliosa
Warszewiczella flabelliformis
Scaphyglottis sp.

In those places where the monte is dense, certain ferns are found on the trees, such as: *Polypodium chnoodes*, *Polystichum adiantiforme* and *Ophioglossum palmatum*. Climbing over trunks of the trees, we also found *Polypodium astrolopes*, *P. lycopodioides* and *Lycopodium linifolium*.

VEGETATION OF LA MENSURA

Certain additions and comments follow concerning the vegetation of the highest peak of Sierra de Nipe, Loma La Mensura. La Mensura, 1,000 m. high, rises abruptly from the plateau of Pinar de Mayarí, which is 600 m. in elevation (Fig. 24). The difference in elevation is not enough by itself to produce any great notable difference in the vegetation of the two mentioned areas. Nevertheless we found a group of plants endemic to La Mensura. Similar conditions prevail with respect to the Gurugú and the Estrella hills, whose vegetation is interrelated with that of La Mensura. The eastern slopes of those peaks hold the typical pinar vegetation. As one ascends La Mensura, the pine becomes rare, and the soil is serpentine as in the charrascal. Nevertheless the typical species of the charrascal are not found here, but instead a group of small plants that are mainly herbaceous. Among the plants of the serpentine on the upper slopes of La Mensura are:

Scutellaria havanensis
Rhynchosia nipensis (creeper)
Metastelma hamatum
Passiflora cubensis (creeper)
Passiflora stenoloba (creeper)
Heptantherus cordifolius
Vernonia angustissima
Cassia lineata
Sonchus oleraceus
Capsicum baccatum
Salvia cubense

Galactia revoluta (creeper)
Stenorrhynchus squamulosus
Habenaria strictissima var.
odontopetala
Chaptalia media
Chaptalia nipensis
Turnera diffusa
Andropogon gracilis
Paspalum rupestre
Aristida refracta
Arundinella confinis

Near the summit of the mountain, as the vegetation becomes more dense, the shrubs are larger than those previously mentioned, and include:

Zanthoxylum dumosum
Anaethaphia lomensis
Anaethaphia menaurensis
Baccharis shaferei
Xolisma obtusa
Oxygonium rosmarinifolium
Anona sclerophylla

Senecio trichotomus
Byrsonima biflora
Guettarda shaferei
Hypericum ascutellatum
Anaethaphia shaferei
Anaethaphia attenuata
Schelia lithosperma

Frequently these shrubs disappear at the summit of these hills, and then a grass *Arthrostylidium capillifolium* produces a dense sward, upon which may be found an interesting orchid, *Oncidium variegatum* (Fig. 25).



FIG. 25. View of the top of La Mensura, where *Arthrostylidium capillifolium* covers the rocky serpentine soil. Note the fog covering the pine land down in the pinar de Mayari plateau.

The western slopes of La Mensura are covered with a wet monte, formed by a large number of small trees, varying from 3-8 m. high, giving to the community a dense aspects. Epiphytes or lianas are apparently not common here. The most frequent tree species, forming the upper layer of this monte, are:

Ouratea revoluta
Hyeronima nipensis
Guettarda monocarpa
Calophyllum antillanum
Tabebuia pachyphylla
Nectandra coriacea
Euchenia capitata
Eugenia nipensis
Dicellaeanthus

Tabebuia nervosa
Juniperus barbadensis
Podocarpus aristulatus
Psidium jarroviifolium
Calophyllum calabazarium
Cordia nipensis
Belairia nipensis
Bimelia revoluta

Smaller trees or shrubs in this monte are:

Psychotria graminifolia
Coccoloba nipensis
Machaonia minutifolia
Calliandra formosa
Lagetta pauciflora
Psychotria evenia

Linociera axilliflora
Ilex pubipetala
Calyptranthes rupicola
Cassia shaveri
Coccoloba cubensis
Psidium wrightii

SAO

As indicated earlier in this paper, the Sierra de Nipe is surrounded by a frame of limestone, which is more



FIG. 26. *Coccothrinax muricata* var. *savannarum*, covering the top of the calcareous cliffs at Cayo del Rey.

noticeable in the western part and specially in the northwest, between Cayo del Rey and Sabanita (Figs. 12 and 14). In this last region, there are vertical cliffs about 80 m. high, and these are covered with an interesting calcicolous vegetation. This community is known locally as sao, and its floristic composition indicates its xeromorphic nature. In this community both small and large shrubs are woody, somewhat microphyllous and spiny. On the upper part of these cliffs, a palm, 1-2 m. high, seems to be frequently a predominant, *Coccothrinax muricata* var. *savannarum* (Fig. 26). Among the most frequent shrubs in this community, are:

Malpighia horrida
Anacardium occidentale
Jacquinia robusta
Lantana camara
Ternstroemia peduncularis
Acidocroton ekmanii
Siphocampylus manettiaeflorus
Myrtus ekmanii
Malpighia suberosa
Hibiscus cryptocarpus

Portlandia polyneura
Eupatorium polystichum
Waltheria americana
Neurolaena lobata
Eugenia pinetorum
Pseudocarpidium rigens
Schmidtottia dephnoides
Ottoschulzia cubensis
Rhytidophyllum tomentosum

Among these shrubs, and creeping over rocks, occur, such plants as:

Dioscorea cubensis
Cissus nipensis
Margarita evenia
Canavalia cubensis

Metastelma sphaeroides
Gesneria montevidensis
Pitcairnia cubensis

MONTE OF THE CALCAREOUS SOILS

Both to the north and south of Cayo del Rey, the calcareous cliffs that surround the Sierra de Nipe, are lower and covered in part by soil, giving origin to a typical monte of the calcareous soil. This monte is not dense, permitting us to find a great number of shrubs and small trees under the large trees that form the upper canopy. The trees of the upper canopy are 25-35 m. high, having quite large trunks and numerous branches. The most frequent tree species of this community are:

Ceiba pentandra
Cecropia peltata
Ochroma lagopus
Gymnanthes lucida
Andira jamaicensis
Didymopanax morototoni
Copaifera hymenaeifolia
Eugenia floribunda
Gilbertia arborea
Spondias mombin
Swietenia mahagoni

Tabebuia angustata
Lonchocarpus latifolius
Elaphrium simaruba
Sapindus saponaria
Buchenavia capitata
Hibiscus tiliaceus
Cassia robiniaefolia
Zanthoxylum martinicense
Cupania glabra
Cedrela odorata

In this locality and especially in the vicinity of Cayo del Rey, we found a palm, *Hemithrinax compacta*, representing an endemic genus of the north coast of Oriente. This palm is about 8 m. high, with a trunk 20-30 cm. in diameter, the leaves of the fan type are 1 m. long, with a petiole similar to that of the genus *Sabal*; the inflorescences which are about 30 cm. long remain almost hidden among the petioles.

SUMMARY

Among the endemic areas of Cuba, the northeastern mountain regions appear to have the highest number of endemic plants. To the present date, there have been described from this region sixteen endemic genera and a large number of species that may repre-

sent about 80 percent of the entire vegetation. Of these genera, some belong to highly endemic families as: Compositae, Rubiaceae, and Acanthaceae. Many of the other genera, however, are very typical and seem to be relict-genera. Among the endemic species of other genera there is also a great number that seem to be relict species. However, we also recognize that the edaphic factors are to be taken into consideration, since a great part of the vegetation is apparently composed of merely neo-endemic or vicarious species. There is also a group of plants, especially the arboreal species, which are common to the whole Cuba. Other species and genera belong to the whole West Indies.

A general study of the vegetation of Sierra de Nipe develops a striking difference from the vegetation of other regions of Cuba, and it does not show that typical affinity which the rest of the vegetation of Cuba has with other areas of the Caribbean region. Considering the geological history of the northeastern region of Cuba, and by closely observing the components of its vegetation, we conclude that we are in the presence of a relict-area.

In a study of the vegetation of Sierra de Nipe, we have distinguished eight communities, most of which we refer to by their vernacular names, as pinar, charrascal, sabana, sao, and monte; other communities here described are, the hygrophylous community, the monte of the calcareous soils and the vegetation of La Mensura. Among these communities, the most important are the pinar and the charrascal. The pinar is a community with a great resemblance to the vegetation of the temperate climate. Here the arborescent dominant is a single species, *Pinus cubensis*, and the herbaceous element is represented by a large number of grasses and sedges. The charrascal, on the contrary, is a typically tropical community, formed by a group of numerous woody shrubs and small trees which make an almost impenetrable thicket. It is in this latter community where we find the largest number of endemic species of the region.

Some other communities as the monte and the hygrophilous are of great floristic importance, and they must be credited with having also a large number of endemic species.

APPENDIX

In addition to those endemic species of Sierra de Nipe collected by us and which have already been presented in the preceding sections of this paper, it is our desire to present here an additional list of endemics of this region which have come to our attention by reading and herbarium work, but have not been collected by us. This list is possibly not an authoritatively complete one.

Alvaradoa psilophylla
Astephanus schlechterianus
Auerodendron cubense
Brunfelsia pluriflora
Caesalpinia nipensis
Calyptrocalyx ekmanii
Calyptrocalyx canapensis
Calyptrocalyx bialata
Calyptrocalyx elongata

Mettenia lepidota
Mimusops mayarensis
Mouriria monantha
Myrcia pungens
Myrcia retivenia
Myrtus oligantha
Oldenlandia polyphylla
Ossaea ekmanii
Ossaea ovatifolia

Calyptrocalyx heterochroa
Calyptrocalyx monocarpa
Calyptrocalyx paradoxa
Calyptrocalyx polyneura
Calyptrocalyx oblanceolata
Calyptrocalyx ramosissima
Casarea crassinervis
Cestrum buxoides
Chiocoba cubensis
Coccoloba acutissima
Croton incrustatus
Dendrophthora nipensis
Erythroxylon lindleyanum
Eugenia bayatensis
Eugenia beyeri
Eugenia canapensis
Eugenia cupuligera
Eugenia exicica
Eugenia leiophloea
Eugenia ligustroides
Eugenia mensurensis
Eugenia piedraensis
Eugenia sterophylla
Eugenia woodfordiana
Fagra namophylla
Gonolobus nipensis
Haenianthus varifolius
Hygrophila bayatensis
Hyperbaena obovata
Ilex grisebachii
Ilex hypaneura
Ilex repandoides
Ipomea erosa
Ipomea platyclada
Krobia nipensis
Labatia micrantha
Leucroton comosus
Leucroton dictyophyllus
Malpighia apiculata

Ossaea pilifera
Pachyanthus discolor
Pachyanthus lindmanii
Pachyanthus mayarensis
Pimenta cubensis
Phyllanthus chamaecristoides
Phyllanthus comosus
Phyllanthus estrellensis
Phyllanthus excisus
Phyllanthus formosus
Phyllanthus incrustatus
Phyllanthus nordii
Phyllanthus phlebocarpus
Phyllanthus shaferi
Plinia punctata
Plinia stenophylla
Plumeria estrellensis
Plumeria stenophylla
Psidium paucinerve
Reynosia truncata
Rhamnidium nipensis
Rhamnidium sulcinerve
Rondeletia diplocalyx
Rondeletia paucinerve
Rondeletia plicatula
Salacia nipensis
Spathelia lobulata
Spathelia stipitata
Stenandrium ekmanii
Stenandrium glabrescens
Tabebuia cuneifolia
Tabebuia exia
Tabebuia furfuracea
Tabebuia mopotensis
Tabebuia nervosa
Tabebuia subcordata

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LIMNOLOGICAL CONDITIONS IN ICE-COVERED LAKES, ESPECIALLY AS
RELATED TO WINTER-KILL OF FISH

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LIMNOLOGICAL CONDITIONS IN ICE-COVERED LAKES, ESPECIALLY AS RELATED TO WINTER-KILL OF FISH

INTRODUCTION

In most fresh-water lakes of the higher latitudes of the temperate regions, winter brings about a set of conditions which differ sharply from those which prevail during the rest of the year. The ice cover, existing continuously for several weeks, and often blanketed by snow, rather effectively separates the body of water from the world above it, and makes it more certainly than ever a microcosm. Several otherwise normal processes are affected or suspended by this ceiling of ice and snow. Aeration of the water by the agitation of wind and wave is precluded, and exchange of gases with the atmosphere by bubbling and diffusion is greatly reduced. Heat exchange between air and water is interfered with, and the amount of transmission of light into the water becomes lowered, sometimes almost to the zero point.

The biotic consequences of these changed conditions are many and varied. The extreme stagnation that at times develops in the water may bring harm or death to countless organisms. Such a mortality, particularly when it is of fish, is known as winter suffocation, or winter-kill.

Since winter-killing may occur frequently, it is perhaps not the most common cause of death of fish, nor that responsible in the long run for the greatest loss; but undoubtedly it is one of the most spectacular, as well as one of the most intensive. The appearance of piles and windrows of dead fish along the shores of a lake, at the breakup of the ice, is dramatic evidence of the harshness and suddenness with which the forces of nature can act. And when a considerable portion of the kill is made up of game and food fish, as it often is, the mortality assumes a serious aspect from the standpoint of fisheries management.

The significance and importance of the winter-kill problem was forcefully brought to the attention of those interested in Michigan fisheries by the extensive and heavy mortality which took place in 1935-36. During the winter of that year a considerable number of lakes in southern Michigan were affected, and hundreds of thousands of fish died. Scenes such as those shown in Figure 1 were common.

During that winter, the Michigan Institute for Fisheries Research carried out a certain amount of preliminary investigative and attempted rescue work. Experiments were performed in aeration of the water by pumping a stream of water into the air and allowing it to run back into the lake through holes chopped in the ice. In other experiments, long holes were cut through the ice, in the hope that atmospheric oxygen would enter the water through surface agitation.

These emergency aeration experiments met with little apparent success. However, the work of that winter emphasized the desirability of an extended



FIG. 1. Winter-killed fish, drifted along the shore of Green Lake after the breakup of the ice, 1936.

study of the winter-kill problem. Accordingly, the Institute arranged for such an investigation. The studies were carried out during the winters of 1937-38, 1939-40, 1940-41, and 1942-43, by the author, under the support of an Institute fellowship, and as a graduate research problem in the University of Michigan. This paper is a report on those studies, not only as they pertain directly to winter-kill, but also as they contribute to the knowledge of general limnological conditions in ice-covered waters.

Rather understandably, but none the less unfortunately, winter work in limnology and fisheries biology has been comparatively scanty in the past. The press of other duties, the difficulties of adapting apparatus and technique to work at freezing temperatures, and the physical hardships of winter weather have combined to keep many research workers indoors at a season when much useful and interesting information is to be found in the field.

ACKNOWLEDGMENTS

The investigation here reported could not have been performed without the generous assistance of many persons and agencies. Particular acknowledgment is given to the Institute for Fisheries Research, of the Michigan Department of Conservation, for financial support and for interest and encouragement, to A. S. Hazzard, its director, for able direction of the work, and to its staff and employees for assistance in many ways.

Gratitude is due to Professor Carl L. Hubbs, formerly of the University of Michigan, for help and guidance throughout the investigation. Helpful advice was received from many other faculty and staff members of the University.

The Associated Tackle Manufacturers, through a trust fund, provided substantial financial assistance to the work. Voluntary help in field work was received from several fisheries students at the University of Michigan.

HISTORICAL

There is little doubt that winter-kill of fish has been observed at various times for perhaps many centuries, since its occurrence is of a very striking nature. It is only within comparatively recent years, however, that very many references to winter fish deaths have entered the general biological literature. A few of these reported observations are cited.

Lühder (1871) described an instance of winter-kill in Germany in 1870-71. In 1871-72 a heavy mortality of fish took place in the Racine River, Wisconsin, where very large numbers of fish, including a large proportion of bass and pickerel, perished (Hoy 1872). Knauthe (1899) reported the winter-kill of many fish in certain artificially enriched carp ponds in Germany. In the Illinois River fish mortality in winter has occurred probably many times; it was recorded for the winter of 1894-95 by Kofoed (1903), and for the winter of 1924-25 by Thompson (1925), who stated that it is of common occurrence. Evermann & Clark (1920) recorded a winter death of fish in Lake Maxinkuckee, Indiana, some time during the period of their investigations there, 1899 to 1908. In Lake Yskjärvi, Finland, a "wholesale mortality" during the winters of 1915, 1922, and 1924 was reported by Jääskeläinen (1930).

In more recent years, winter-kill, sometimes of considerable intensity, has been reported from various places, some of which are: Massachusetts (Sweetman & Warfel 1936), Iowa (Aitken 1938, Sheppard 1938), Minnesota (Olson 1932, Smith 1941), and Utah (Higgins 1933).

The locations of the most serious instances of winter-kill in Michigan which have been satisfactorily reported for the period 1930 to 1941 are shown on the map of Figure 2. No accurate, dated records of kills prior to 1930 are available, although many oral communications from local residents indicate that heavy mortalities occurred in various lakes in winters of many years past.



FIG. 2. Instances of winter-kill reported in Michigan, 1930-1941.

Many of the phenomena connected directly or indirectly with winter suffocations have been recognized and understood, although sometimes rather imperfectly, by various previous workers. The literature contains a fairly large number of references to conditions in stagnant water under the ice, including some mention of the causes and effects of winter-kill. Although some of these writings are based upon actual observation, many others consist in large measure of hypothesis and conjecture, partially or wholly unsubstantiated. That many of these hypotheses later have been proved to be true is a favorable commentary upon the soundness of the original supposition. That others have been found to be unsound or even absurd points to the lack of information upon which they were based. One of the objects of the present study has been to obtain data which might contribute either to the proof or to the disproof of some of the theories and notions which have been proposed concerning the subject. A brief summary of some of these ideas follows.

The function of an ice cover in preventing aeration of the water by wind action is obvious. It was recognized by as early an author as Hoy (1872), and has been mentioned by numerous writers since. That ice, if it is thick or cloudy and especially if it is covered with snow, has another serious effect, in diminishing the transmission of light needed for photosynthesis, was understood quite clearly by Knauthe (1899). This effect has been reaffirmed by many authors: by Birge & Juday (1911), Olson (1932), Welch (1935),

Titus (1936), Aitken (1938), and Hubbs & Ehmeyer (1938), to mention only a few.

The connection between winter stagnation and the abundance of organic materials in a lake has been pointed out by Drown (1892), Knauth (1899), Welch (1935), and others; and various authors (Thompson 1925, and others) have called attention to the fact that critical conditions are more apt to obtain in shallow lakes than in deeper ones.

Most of the authors have assigned the primary blame for the winter death of fish to diminished dissolved oxygen content of the water, but several papers have mentioned other factors as being chief or contributing causes. Hoy (1872) stated that the death of many of the fish in the Racine River was "caused, probably, by the poison communicated to the water by the multitude of decaying minnows." Wickliff (n.d.) added to the lowered oxygen tension the presumed toxic effect of carbon dioxide, nitrogen, ammonia, and hydrogen sulfide. A popular point of view, expressed in the Milwaukee Sentinel (1939), referred to the "poisonous gases which mean death to the fish." In regard to the winter mortality of fish in acid bog waters, Jewell & Brown (1929) assumed the cause of death possibly to be either depletion of oxygen or the "production of toxic substances due to putrefaction."

WATERS INVESTIGATED

The major part of the field work of the present study was done on Clear Lake, Mud Lake, Green Lake, Bog Lake, and on a private farm pond, Pasinski's Pond, all in southeastern Michigan. These waters are listed in Table 1, and also are briefly described below. During part of one winter, Richmond Lake was under observation; also certain experiments, to be described later, were conducted in some small experimental ponds at the Drayton Plains state fish hatchery. Various other lakes in the southern peninsula of Michigan were used for occasional or single observations.

Clear Lake, Mud Lake, Bog Lake, and Green Lake lie within that part of Washtenaw and Jackson counties which has been designated the Waterloo

Area, a region of generally poor farm land which was developed for several years by the U. S. Park Service as a recreational area. This area is in heavily glaciated territory, characterized by a rather rugged topography, abrupt transitions in soils types, and many and varied bodies of water. Within the Waterloo Area are several shallow lakes of the type which is apt to be subject to winter-kill.

Pasinski's Pond, in Livingston County, is also in a region of numerous lakes and pot-holes.

Table 1 gives some of the principal physical characteristics of the lakes studied. All of them, with the exception of the dystrophic Bog Lake, are in the eutrophic class, according to the Thieneman-Naumann system. Since eutrophic lakes vary greatly in organic richness, without sharp dividing lines, the lakes under study can be subdivided only in general, relative terms.

CLEAR LAKE

Clear Lake is surrounded by steep wooded hills, and has only a vague stream connection with any other body of water, receiving most of its water supply from surface and sub-surface run-in. Its morphometry is shown by the map (Fig. 3). The name of the lake is fully justified by the clearness of its water; a Secchi disc can be seen at 20 to 25 feet. There is considerable rooted vegetation in the shallower parts of the lake. The bottom contains a substantial proportion of marl. Compared to most of the lakes of the region, Clear Lake is relatively little advanced in eutrophy; in point of view of several characteristics, it is not far beyond the border-line between oligotrophy and eutrophy.

No winter-kill has ever been recorded for the lake. Hence it was included in this investigation as an example of those lakes of the general region which do not develop winter-kill conditions, so that comparative data might be secured which would demonstrate some of the difference between these lakes and lakes typically subject to winter-kill.

MUD LAKE

This lake, as shown by Figure 4, is uniformly shallow, with no water over about 5 feet deep. It is surrounded by wooded hills and grassy marsh. It normally has a flowing inlet and outlet. Thus there is somewhat of a current through the lake, modifying many of its conditions. Otherwise its characteristics are rather typically those of many southern Michigan lakes. The water is moderately clear. Much of the bottom is composed of soft, organically rich material, with some marl areas. The lake produces a reasonably large amount of fishing for largemouth bass and panfish.

GREEN LAKE

The size, shape, and depth of Green Lake, and the location of sampling stations, are shown by Figure 5. The lake has a small but steady inlet, which carries seepage water from a large marsh. Most of the lake is shallow, less than 10 feet deep, with dense rooted vegetation.

TABLE 1. Principal lakes studied; physical characteristics.

Lake	Area, Acres	Max. Depth, Feet	IN WINTER		Rooted Vegetation, Distribution	Methyl Orange Alkalinity, Usual range, p.p.m.	Class
			Inlet	Outlet			
Clear.....	140	35	No	No	Limited	150-180	Early-stage eutrophic
Mud.....	62	5	Yes	Yes	Widespread	200-260	Mid-stage eutrophic
Green.....	78	10	Yes	Yes	Widespread	170-210	Mid-stage eutrophic
Richmond.....	15	10	No	No	Widespread	140-160	Late-stage eutrophic
Pasinski's Pond.....	4	5	No	Yes	Total area	123-200	Late-stage eutrophic
Bog.....	1/4	6	No	No	Absent	5-10	Dystrophic

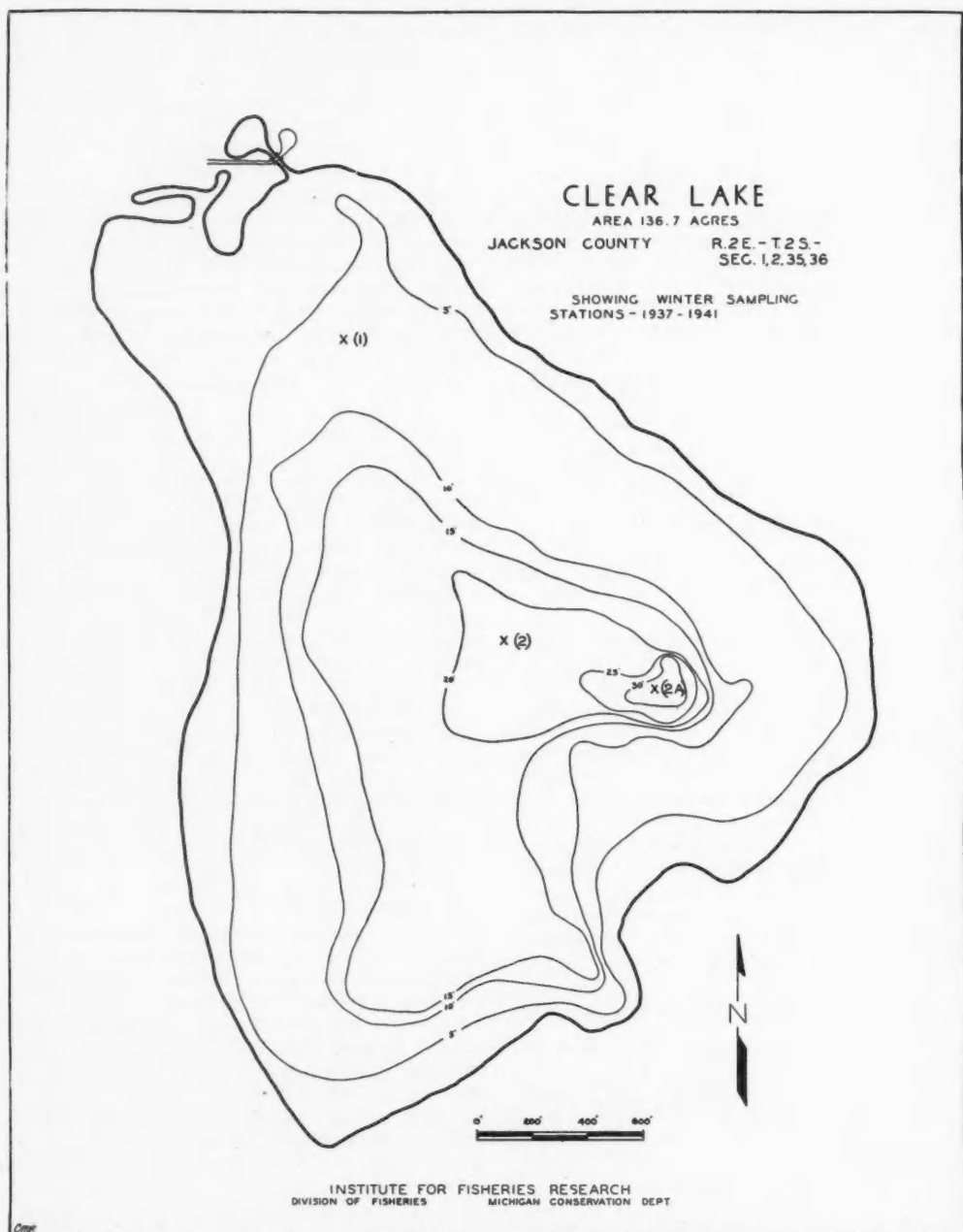


FIG. 3. Clear Lake. Sampling stations indicated by x ().



FIG. 4. Mud Lake. Sampling stations indicated by x ().

The lake is semi-artificial, being enlarged a few years ago by the construction of an earth dam. The newly flooded bottom as well as that of the original basin, is very rich in organic material. The lake has suffered severe winter-kill of fish in several years. However, it has retained or been artificially restocked with a sufficiently large population of game fish to provide good fishing.

BOG LAKE

The small pot-hole here called Bog Lake is a typical brown-water acid bog lake. No map is available. The lake is about $\frac{1}{4}$ acre in size, and oval in shape. At its present level, it is isolated from any other body of water; but at the slightly higher level which probably existed at some time in the past, it had an outlet. Its greatest depth, 6 feet, prevails over most of its area, since the slope of the shore is abrupt.

Bog Lake fits quite well the general conception of a lake of the dystrophic type, and conforms well to the definition given by Welch (1935) for a bog lake. Its water is stained a dark brown, is very soft, and moderately acid. The bottom material is gelatinous

and flocculent, although there is not a false bottom such as that which occurs in many bog lakes. The only species of fish known to live in Bog Lake is the mud minnow, *Umbra limi*. Nothing has been recorded concerning possible winter-kill of fish in this lake.

PASINSKI'S POND

This private pond was constructed about 1932, by damming a natural valley. It has no inlet, but receives surface drainage from grassy hillsides, and is fed by underground seepage. A small motor-driven pump on the east shore of the north end of the pond, capable of delivering approximately 60 gallons per minute from a shallow well, is used at times to help maintain the water level. There is a small outlet which flows except at times of drouth.

As shown by the map, Figure 6, the pond has an area of about 4 acres, and a maximum depth of 5 feet. Its soft bottom has a high organic content. The water is choked with rooted water plants, the bulk of which consists of the waterweed, *Anacharis*. There is also a considerable amount of filamentous algae, most of which apparently is *Spirogyra*. The amount of algae present in a growing condition varies

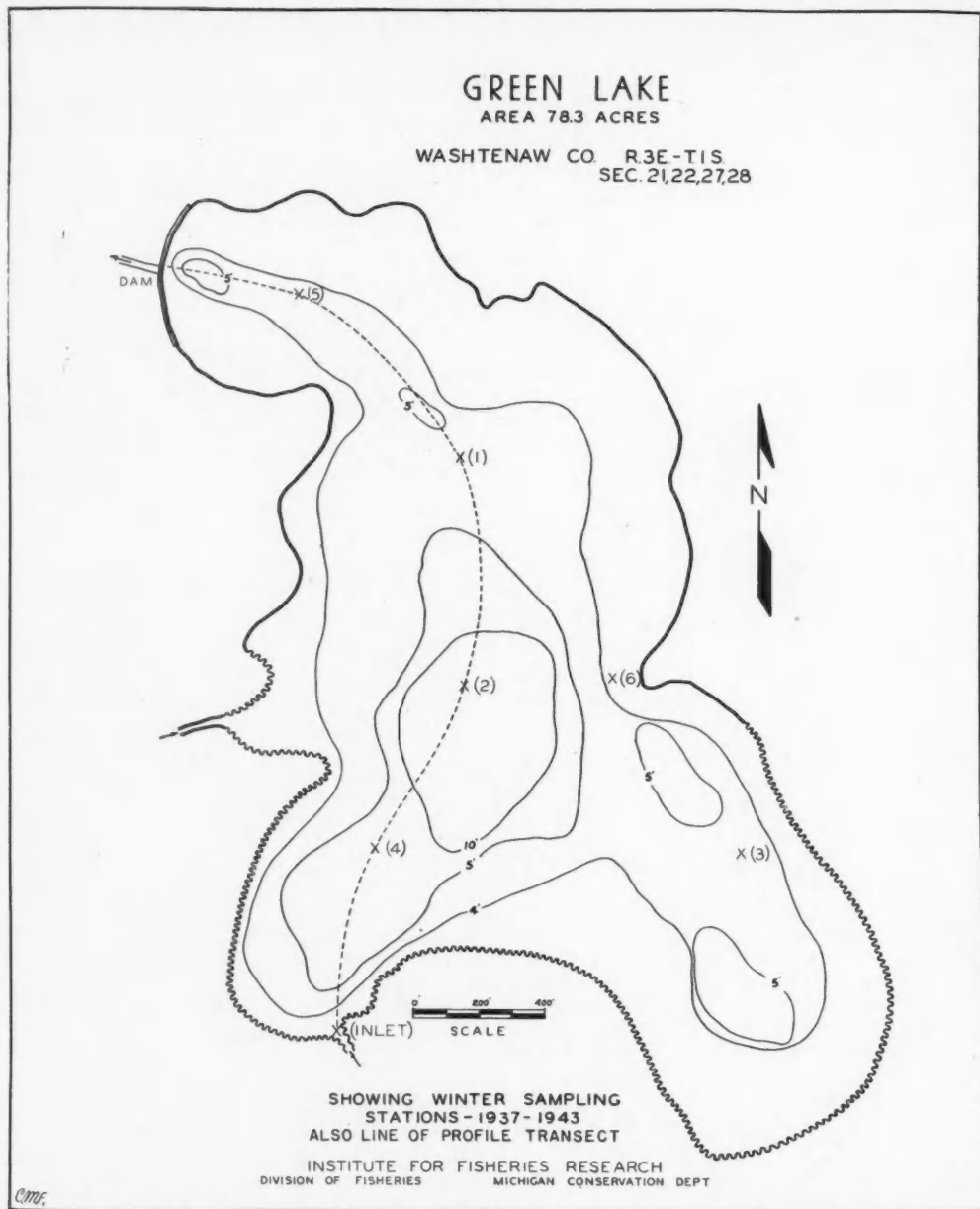


FIG. 5. Green Lake. Sampling stations indicated by x (), and profile section by broken line.

from one time to another, but is nearly always greater in the end of the pond nearest the outlet (the south end) than in that nearest the pump (the north end).

The pond has been the site of various activities of the Institute of Fisheries Research. It was poisoned in 1937 and 1938, in an attempt to destroy the abundant population of bullheads, *Ameiurus nebulosus*, which was then the only species of fish present. Large numbers of bullheads were killed, but an unknown

number survived. The pond was stocked, in 1938, with bluegills.

In the winter of 1939-40 a heavy winter-kill took place in the pond, apparently totally destroying the bluegill population, and killing many bullheads. Winter-kill in previous years has been reported, and in the summer of 1937 a large number of fish were reported to have died because of summer stagnation.

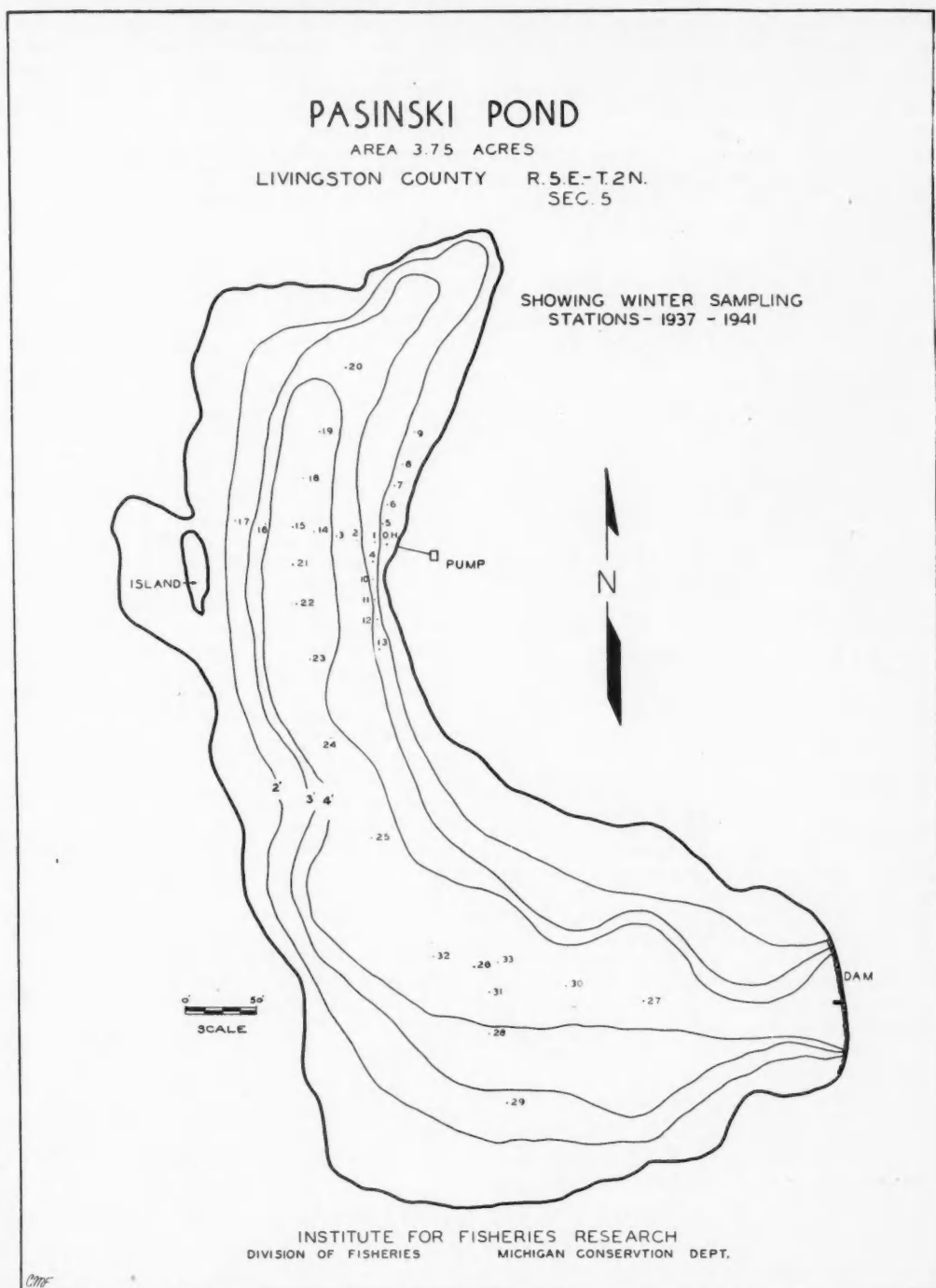


FIG. 6. Pasinski's Pond. Sampling stations numbered.

RICHMOND LAKE

Richmond Lake is a small, shallow lake, extremely rich in organic materials, with a bottom of soft mucky material, which at times becomes putrescent. The lake apparently is filling in rather rapidly, and already may be considered to be well advanced in senescence.

The lake was studied only in the winter of 1939-40, and at a time when serious conditions already had developed. There was a considerable loss of fish that winter. Nothing is known concerning previous winter-kills.

HATCHERY PONDS

For some experiments described below, three small experimental ponds at the Drayton Plains hatchery were used. These ponds are entirely artificial and are very nearly alike. Each is 50 by 100 feet, with a fairly uniform depth of 3 feet. The bottom is soft mud, and the rooted vegetation is limited. The ponds may be filled with water from the Clinton River, and they have overflow outlets.

PROCEDURE, METHODS, AND EQUIPMENT

SAMPLING STATIONS

During the course of the investigation, a large number of sampling stations were established. Some of these were used continuously throughout the study, some for only one or two winters, and some only once or a few times.

In Clear Lake, a shallow station (Station 1) and two deeper ones (Stations 2 and 2a) were used.

The original Station 1 of Mud Lake was used in three winters. In two of these winters, samples were taken from three other stations and from the inlet and outlet streams.

Likewise in Green Lake the original Station 1 was sampled throughout the study, and for some of the work other stations, including Stations 2 and 4 in deeper water, were used. In the winter of 1939-40, a hole in the ice, a few feet across, was artificially kept open for a few weeks.

Locations of the various stations on Clear, Mud, and Green Lakes are shown on the maps of Figures 3-5.

In Pasinski's Pond, Station 15 in the north end, and Station 26 in the south end, became the principal routine sampling stations, but for some experimental work on the pond in 1939-40, described below, over 30 additional stations were used. These are shown on the map of Figure 6. The open hole of 1939-40 was near the point of discharge of the pump.

The depths of sampling were not entirely constant. They were affected somewhat by variations in lake water level, and by slight changes in station location. Although the stations were marked with stakes set into the ice, their exact positions changed slightly from time to time, and of course varied somewhat from winter to winter.

The primary sampling depth at each station was that designated as "surface" or "top." This sample was taken at from 4 to 6 inches below the surface

of the water as it stood in the hole chopped through the ice. Although this level at times may have been above the under surface of the ice, it is assumed that it held water which previously had been just under the ice, and which had flowed into the hole.

The sample of next importance at any station came from about $\frac{1}{2}$ to 1 foot above the bottom, this level being the deepest at which the sampler could be operated without stirring up the bottom materials. This sample is called "bottom." At many stations, samples also were regularly taken at various intermediate depths.

SAMPLING

The lakes were sampled periodically, each winter, throughout the entire period when the ice was safe to walk on. Whenever the ice was thick enough to permit doing so, an automobile was driven onto the lakes. At other times either a portable shanty or a specially fitted hand sled was used. Both the shanty and the sled were equipped with gasoline lanterns to prevent water samples from freezing.

The hole for sampling was made beside the station marker, or at a short distance, where average conditions of ice and snow existed. The hole, from 8 to 10 inches in diameter, was cut with a steel ice-spud, and care was used to minimize the agitation of the water by upwelling.

Samples of water were taken with a sampler modified somewhat from that figured in Standard Methods (American Public Health Association 1936, p. 140). The sampler consists of a metal can, in which the sample bottle sits, with tubes for delivery of water and escape of air, so arranged that the volume of water in the bottle is displaced at least three times, without the entrainment of air bubbles. For winter work, this sampler was found to be superior in many respects to the Kemmerer bottle. It is much less subject to freezing, and it is more sturdy and can better withstand handling under the ice. Since it is more compact, it can take a sample from a thinner stratum of water, and from nearer the bottom.

When samples were taken at more than one depth at a station, an almost unvarying procedure was employed. The sample from the surface was taken first, followed by that from the next lower depth, and so forth. Thus no layer of water was subjected to agitation, by air bubbling from below it or by the sampler passing through it, before a sample from that layer had been secured.

Water samples were collected in 250-ml., ground-glass stoppered bottles. They were prevented from freezing, but were kept at a low temperature until their analysis had been completed.

DISSOLVED OXYGEN

Dissolved oxygen was determined in 1937-38 by the Rideal-Stewart modification of the Winkler method. This modification is extremely tedious at near freezing temperature, so in later winters the rapid modification of the Winkler method, for waters containing organic matter (Standard Methods 1936, p. 145), was used. The procedure up to and including acidification was

carried out in the field, sometimes at the station, but more often after the sample had been taken to shore. At low temperatures, it is likely that no significant change in the dissolved oxygen content of water in a tightly stoppered bottle takes place in an hour or two (Birge & Juday 1911, p. 17). The samples were titrated, after transportation to the laboratory, within a few hours and without having been allowed to warm up.

Results of the dissolved oxygen determinations are expressed in parts per million (p.p.m.). It is probable that this expression has a more significant meaning than does percent saturation. At any rate, since the temperature of the water under the ice stays within rather narrow limits, the two sets of figures are closely proportional.

pH, CARBON DIOXIDE, ALKALINITY

The pH was measured colorimetrically, using a spot-plate, pipette type pH set. Free carbon dioxide was determined by titration with standard alkali in the presence of phenolphthalein indicator. Total alkalinity (methyl orange alkalinity) was measured by titration with standard acid, using methyl orange as an indicator.

BIOCHEMICAL OXYGEN DEMAND

Biochemical oxygen demand was determined by constant temperature incubation in 250-ml. ground-glass stoppered bottles. The method used was that of the U. S. Public Health Service (Theriault 1927, American Public Health Association 1936), with considerable modification and simplification. Undiluted samples were used whenever possible; when dilution was necessary, the preference in calculating weighted mean values was given to the sample least diluted. A dilution of 1:2 often sufficed, and the greatest dilution necessary, even with samples having a high oxygen demand, was 1:5. All dilutions were made with aerated distilled water, without bacterial seeding. Since the dilutions were not great, it is rather probable that sufficient bacteria, as well as inorganic nutrients, were supplied by the water sample. All the results are expressed in parts per million.

B.O.D. measurements were made at two incubation temperatures; at the standard temperature of 20° C., giving results that may be compared with those of other investigators, and at 0° C. (rather, just above 0°), which temperature closely simulates natural conditions under the ice. Incubation at 20° was performed in an electric incubation, and at 0° in a household electric refrigerator. Most of the samples were incubated for the standard 5-day period; but one series was incubated for 60 days.

LIGHT PENETRATION

Measurements of the penetration of light through water, ice, and snow were made with a specially designed submersible photometer, employing photoelectric cells. In recent years this type of photometer has come into rather common use, particularly in oceanography. Many different designs have been em-

ployed (Ellis, 1934, Pearsall & Ulyott 1933, Burr & Burr 1934, Utterback & Wilson 1940, etc.). All, however, embody photoelectric cells of the selenium rectifier, or similar, type. They differ mainly in external design.

The photometer used here (see Figures 7 and 8) was built with special adaptations for use under ice.

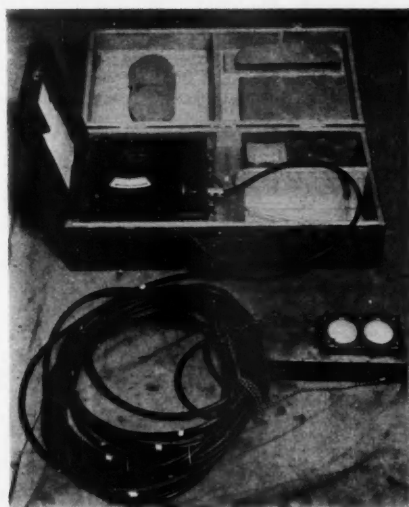


FIG. 7. Submersible photometer, with cable and microammeter.

It consists of a suitably housed receiver, using two Weston "Photronic" cells, and connected by a waterproof cable to a very sensitive multiple-range galvanometer. The brass housing case of the receiver can be fitted with a detachable pipe handle, enabling it to be thrust under the ice to a distance of about two feet from the edge of the hole which must be cut into the ice. With the handle removed, the receiver can be lowered and raised by means of the electric cable. In general principle, the apparatus is similar to that described by Zinn & Ifft (1941), but differs in mechanical design, and in using an extra Weston cell for added sensitivity. In optical and electrical detail, it meets the chief specifications of the International Council for the Exploration of the Sea (Atkins et al. 1938).

Between the cells and the water there is, first, a plate glass window, and above that a removable diffusing window made of single opal-flashed glass. The space between the two glasses may contain an interchangeable glass color filter. Also in this space may be inserted a light-reducing filter for cutting down the intensity of light on bright days, so that the readings are not off the scale of the meter. The filter so used for this investigation was made of exposed and developed photographic film (a glass filter would be more durable).

Color filters of three wave-lengths were used, approximating very closely the specified ranges of

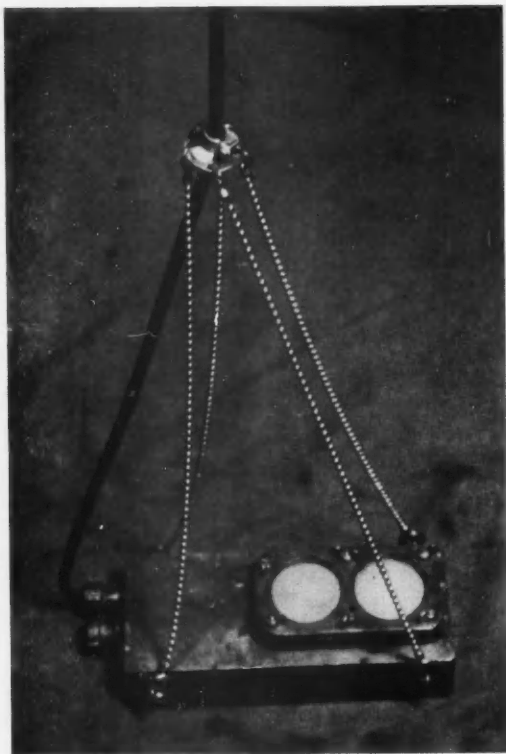


FIG. 8. Target of submersible photometer, showing method of suspension by electric cable.

green red, and blue, as given in Atkins et al. (1938). These colored glasses were obtained from the Corning Glass Works.

The procedure of making measurements of light penetration through ice and snow was as follows. An initial reading was made with the receiver in the air, resting horizontally on the surface of the ice. In recording the data, this reading was termed "air." Then, with as little loss of time as possible, the receiver was thrust under the ice, with the upper face of the receiver held tightly and flatly against the under surface of the ice, and a reading was taken. In the data tabulation, this reading is called "ice." Another reading was taken in the air, another under the ice, and so forth, sufficient alternating readings being made to make sure that the intensity of daylight had remained reasonably constant throughout the process. If measurements at various depths in the water also were made, the same alternating procedure was followed.

It was found that on either completely cloudless days or heavily overcast days the light remained sufficiently constant to provide acceptable results over periods long enough to make the necessary number of readings, and that only times when the sky was partly cloudy needed to be avoided. Utterback

(1933), however, found that at certain times "the intensity of the visible light may vary within a few minutes by several percent, even though there be a cloudless sky and a clear atmosphere." Hence, although considerable precaution was used, it is not impossible that a small error may have entered the results obtained. Measurements were always made at about the same time of day, usually close to noon, to avoid large changes in the angle of light.

Measurements of penetration of light through the snow cover were, of necessity, made indirectly. The penetration through the ice plus snow was measured. Then the snow was removed, and a measurement made of penetration through the ice alone. From these two readings the amount of penetration through the snow alone was computed.

The instrument was calibrated in terms of light intensity in foot-candles incident upon the face of the target, by the use of a standardized photoflood bulb. The temperature correction was ascertained by calibration at several temperatures. It was found, in agreement with the statement of Utterback & Wilson (1940), that the temperature correction is greater at higher illumination levels.

The results are expressed in terms of percentage penetration. This figure is obtained by dividing the amount of light which penetrates through a given layer of ice, snow, or water, by the total amount of light impinging upon that layer. It must be remembered that both these figures, as measured by a photronic cell, are not true total light, since this cell has a maximum sensitivity in the yellow-green portion of the spectrum.

Possible error caused by the loss of low-angle light was not taken into account. Such loss is minimized by the opal glass diffusing window. Furthermore, the various readings are comparable, since the angle of light always was approximately the same.

RESULTS AND DISCUSSION

WEATHER, ICE, AND SNOW

The winter climate of southeastern Michigan is moderately cold, with fairly even precipitation. Snows are apt to be frequent, but rather light. Many days are cloudy or partly cloudy, and there is fair to moderate humidity. There are many winter breezes and light winds, but rarely is there a storm of blizzard-like intensity. Midwinter thaws are frequent, and it is rather seldom that snow remains on the ground continuously throughout the winter.

The time of freezing-over of the lakes in the region not only varies with the size, depth, and exposure of the lake, but also varies greatly from year to year. In the winter of 1937-38 there was an ice cover on some of the lakes studied from December 10 to March 15. In 1939-40 the ice cover did not form until almost January 1, but it lasted until April 5. In 1940-41 the lakes froze over early, some of them being completely covered by December 5. A warm spell in late December partially opened up the lakes for a few days, from December 25 to January 5.

TABLE 2. Thickness of ice and snow on lakes studied.

Lake	Date	Ice, inches	SNOW	
			Inches	Condition
Green...	Dec. 11, 1937	...	Trace	...
	28	8	None	...
	Jan. 5, 1938	9	None	...
	12	9	1	...
	19	10	1	Crusted
	26	12	Trace	...
	Feb. 2	12	None	...
	9	5	None	...
	20	3	Trace	...
	27	2	3	Slushy
	Mar. 8	2
	Jan. 10, 1940	5	2	...
	17	5	$\frac{1}{2}$...
	24	10	1	...
	31	10	2	...
	Feb. 8	10	3	...
	14	10	3	...
	21	...	2	Crusted
	28	...	6	...
	Mar. 8	14	2	Crusted
	11	14	1	...
	16	14	$\frac{1}{2}$	New
	20	12	3	New
	23	...	3	Crusted
	27	12	5	...
	31	8
	Apr. 3	6	None	...
	Dec. 10, 1940	4	None	...
	17	6	Trace	...
	21	5	None	...
	24	3	None	...
	Jan. 1, 1941	Open
	7	4	None	...
	12	6	1	...
	23	8	None	...
	26	8	None	...
	28	10	$1\frac{1}{2}$...
	Feb. 9	10	2	Dry
	14	6	None	...
	24	10	2	Drifted
	Mar. 2	10	1	Drifted
	4	10	$\frac{1}{2}$	Drifted
	8	10	Trace	...
	Dec. 5, 1942	3	None	...
	16	6	$\frac{1}{2}$...
	23	9	1	Crusted
	29	6	None	...
	Jan. 4, 1943	8	2	Dry
	8	8	3	Drifts, plus new
	12	8	3	Dry, firm
	16	9	6	Drifts, plus new
	22	12	10	Dry, over slush
	24	12	Trace	...
	29	12	Trace	...
	Feb. 2	12	1	New, crusted
	5	...	Trace	Nearly gone
	8	12	1	Crusted
	13	12	$\frac{1}{2}$	New
	22	12	None	...
	27	10	None	...
Mud...	Dec. 11, 1937	4	Trace	...
	28	6	None	...
	Jan. 5, 1938	...	None	...
	12	8	1	...
	19	12
	26	12	Trace	...

TABLE 2 (continued)

Lake	Date	Ice, inches	SNOW	
			Inches	Condition
Clear...	Feb. 2	12	None	...
	9	7	None	...
	20	4	Trace	...
	27	4	4	...
	Mar. 8	3	None	...
	Jan. 6, 1940	4	$1\frac{1}{2}$...
	10	5	2	...
	13	5	$2\frac{1}{2}$	Slushy
	17	6	$\frac{1}{2}$...
	20	8	$\frac{1}{2}$...
	24	10	1	...
	28	12	$1\frac{1}{2}$...
	31	10	2	...
	Feb. 3	10	3	...
	8	10	$3\frac{1}{2}$...
	11
	14	10	3	Packed
	18	12	2	Packed
	21	12	2	Crusted
	25	...	2	...
	28	...	6	...
	Mar. 3	...	2	Slushy
	8	12	1	Crusted
	11	12	1	...
	16	12	2	...
	20	10	3	New
	23	12	3	Crusted
	27	12	5	...
	31	8
	Dec. 10, 1940	4	None	...
	19	6	Trace	...
	24	4	None	...
	Jan. 1, 1941	Open
	7	3	None	...
	14	6	1	Crusted
	23	6	None	...
	30	8	$1\frac{1}{2}$...
	Feb. 4	10	None	...
	11	10	$1\frac{1}{2}$...
	23	10	1	...
	Mar. 2	10	1	Drifted
	8	10	Trace	...
Clear...	Dec. 28, 1937	10	None	...
	Jan. 5, 1938	10	None	...
	12	10	$1\frac{1}{2}$...
	19	12
	26	12	Trace	...
	Feb. 2	12	None	...
	9	10	None	...
	20	5	Trace	...
	27	4	$3\frac{1}{2}$...
	Mar. 8	2
	Jan. 6, 1940	4	$1\frac{1}{2}$...
	10	6	2	...
	13	6	3	Slushy
	17	8	$\frac{1}{2}$...
	20	9	$\frac{1}{2}$...
	24	12	1	...
	28	14	$1\frac{1}{2}$...
	31	12	2	...
	Feb. 3	12	3	...
	8	12	4	...
	11	12	6	...
	14	12	3	Packed
	18	12	2	Packed
	21	12	2	Crusted

TABLE 2 (continued)

Lake	Date	Ice, inches	SNOW	
			Inches	Condition
Green Lake	25	14	3	...
	28	...	6	Crusted
	Mar. 8	14	1	Crusted
	11	14	$\frac{1}{2}$...
	16	14	$2\frac{1}{2}$...
	20	14	3	New
	23	14	3	Crusted
	27	14	5	...
	31	10	None	...
	Apr. 3	8	None	...
	Dec. 10, 1940	1	None	...
	15	...	None	...
	21	6	None	...
	Jan. 1, 1941	Open
	7	Thin	None	...
	12	8	1	...
	23	6	None	...
	30	10	$1\frac{1}{2}$	Crusted
	Feb. 6	10	None	...
	14	8	None	...
	23	...	$1\frac{1}{2}$	Drifted
Bog Lake	Mar. 2	10	1	Drifted
	8	10	Trace	...
	13	6	...	Melting
	Jan. 6, 1940	2	2	...
	13	3	3	Slushy
	20	4	$\frac{1}{2}$...
	28	5	2	...
	Feb. 3	5	3	...
	11	4	4	Slushy
	18	4	1	Packed
	25	4	3	...
	Mar. 11	4	$\frac{1}{2}$...
	16	5	$\frac{1}{2}$	New
	23	4	3	Crusted
	27	6	5	...
	Dec. 10, 1940	2	None	...
	17	3	Trace	...
	21	3	None	...
	Jan. 1, 1941	Thin
	7	2	Trace	...
	14	3	1	...
	23	4	None	...
	28	5	$1\frac{1}{2}$...
	Feb. 4	5	$\frac{1}{2}$...
	11	6	2	...
	16	6	$\frac{1}{2}$	New
	25	10	2	Crusted
	Mar. 2	8	$1\frac{1}{2}$	Crusted
	4	8	$\frac{1}{2}$	New
	10	9	...	Hard
	27	6	None	...

After refreezing, the ice remained intact until almost April 1. In the winter of 1942-43 the ice seal lasted from December 1 until after March 20.

Table 2 gives the thickness of the ice on the various lakes of the survey, on the dates on which these lakes were visited. These figures represent, usually, the average thickness over the surface of the lake.

Also given in Table 2 is the depth of snow on the ice from time to time. Obviously, only an approximately average figure can be given, because drifting often caused the snow to be much deeper in some places than in others.

Figure 9 shows the depth of snow throughout the periods of ice cover of the winters 1935-36, 1937-38, 1939-40, 1940-41, and 1942-43. The data of Table 2 were obtained at too infrequent intervals to be adequate for the construction of smooth curves. Therefore they were supplemented by data, secured from the weather station of the University of Michigan, for the amount of snow on the ground, from day to day, in Ann Arbor. Snowfalls in the region usually are general, and the depth of snow tends to be approximately the same (except for drifting) from one place to another.

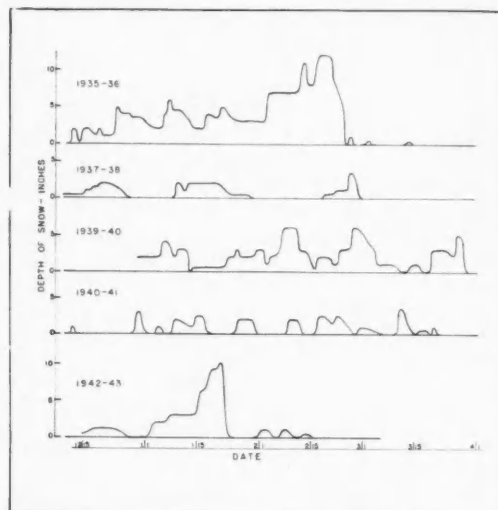


FIG. 9. Depth of snow on the ground in the area studied, during the periods of ice cover.

It is readily apparent from Figure 9 that in the year of the heavy winter-kill, 1935-36, not only was the snow fairly deep, but it remained on the ice for a long uninterrupted period. Likewise in 1939-40, a winter with some kill, although the snow was not so deep, it covered the ice for a rather long unbroken span of time.

In contrast, in the winter of 1937-38, and even more so in 1940-41, the snow on the ice frequently was dissipated by thaw or rain; and hence, although there were many snowstorms, there were no extended periods of snow coverage. These two winters were virtually free from winter-kill in the lakes in the region.

In the winter 1942-43 snows began early, and as the result of one snowfall after another the ice (on Green Lake) by January 20 was covered with 10 inches of snow. At this time much of this snow had become slush, because of melting and of the presence of water on the ice.

Rather suddenly, probably within the space of one night, the ice was lifted, apparently by a change in the water level of the lake combined with the buoyancy of the ice. The water on the ice flowed through

cracks and around the ice sheet, and that part of the slush remaining on top of the ice soon froze into a layer of rough, cloudy ice. The ice was covered with snow only for brief periods throughout the rest of the winter.

It is highly probable that this sudden disappearance of the snow on Green Lake happened just in time to prevent a serious winter-kill, for conditions in the water were fast becoming critical.

WATER TEMPERATURE

Water temperature measurements were made regularly only in one winter. Some general trends were noticed. One evident tendency is toward the development of a very abrupt drop-off in temperature in the upper few feet of water, with a much more gradual decline from there to the bottom. Another is the distinct warming up of the general mass of water as the winter season progresses. Probably an insignificant part of this increase in temperature is due to the oxidation of organic matter, virtually all of it being produced by the radiant energy of sunlight. The occasional entrance into a lake of a considerable amount of comparatively warmer rain water may contribute a small part of the heat.

DISSOLVED OXYGEN

By far the best single indicator of conditions for fish life in the water under the ice is the amount of dissolved oxygen. The determination of dissolved oxygen is a relatively simple and reliable procedure, and one which is capable of adaptation to winter field work. Therefore the data of this study contain a large proportion of dissolved oxygen values.

A relatively large range of dissolved oxygen values was observed, at various times and places. A few of the highest oxygen readings recorded during the survey were: Clear Lake, 16.2 p.p.m., Station 1 on January 20, 1940; Mud Lake, 19.4 p.p.m. (approximately 135 percent saturation), at Station 4 on March 11, 1940; Bog Lake, 21.0 p.p.m. (about 145 percent saturation), on February 11, 1941; and Pasinski's Pond, 28.0 p.p.m. (about 190 percent saturation), at Station 26 on January 31, 1941. During the winter 1940-41 a considerable number of samples from Pasinski's Pond contained over 20 p.p.m. dissolved oxygen.

The most rapid increase in oxygen noted was in Green Lake, at Station 5 at the surface, where the oxygen changed from 1.8 p.p.m. on February 5, 1943, to 9.8 p.p.m. on February 8, an increase of 8.0 p.p.m. in 3 days, or at the rate of 2.7 p.p.m. per day. The most abrupt decline noted was in Pasinski's Pond, at Station 27. Here the oxygen fell from 12.3 p.p.m. on February 12, 1940, to 2.4 p.p.m. on February 14, a decrease of 9.9 p.p.m. in two days, or at the rate of 5 p.p.m. per day.

The oxygen in Clear Lake showed considerably less variation (Figs. 10 and 11) than that in the more shallow, more eutrophic lakes. At Station 1, in Clear Lake, the top and bottom samples were remarkably similar in oxygen content at nearly all times. At the

deeper Station 2 (Station 2a in 1940-41) a much more evident stratification was found. The water layers at the surface, 10-foot, and 20-foot levels had an almost uniform content of dissolved oxygen at the start of the winter of 1939-40, but gradually developed the spread in oxygen values typical of stratification (Fig. 10). Strangely enough, in the winter of 1940-41, the oxygen in the deeper water was rather low even at the onset of the ice cover; the oxygen curves for this station in Figure 11 are almost level throughout the winter. Apparently for some reason stratification already had developed before the first samples of that winter were taken (even though sampling was started two weeks earlier than in the preceding winter). It is possible, although not definitely known to be the case, that following the fall overturn some sort of an oxygen demand (more or less pronounced and rather immediate) developed in the lower water, and that this demand was sufficient to bring about such early stratification.

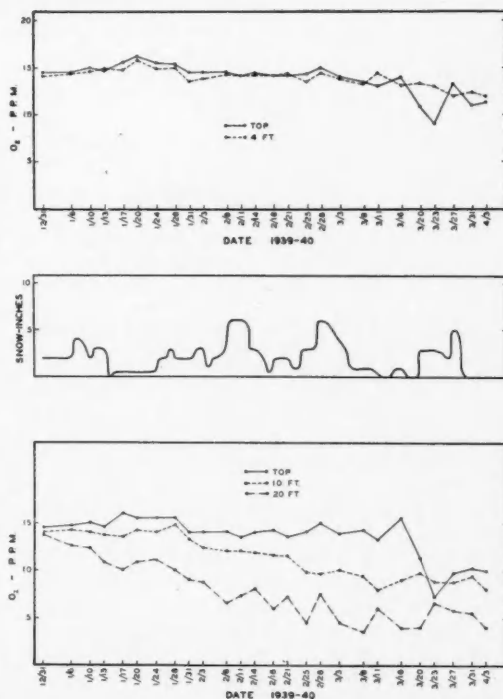


FIG. 10. Dissolved oxygen and snow cover, Clear Lake, 1939-40. Upper curves are for Station 1, lower ones for Station 2.

The greater eutrophy of Mud Lake is reflected in its oxygen curves for 1939-40 (Fig. 12). As may be seen by juxtaposing these curves with the curve which represents depth of snow, there was a definite response in the oxygen value—especially at some stations—to changes in light intensity. Stations 2, 3, and 4 showed low oxygen during the period of snow

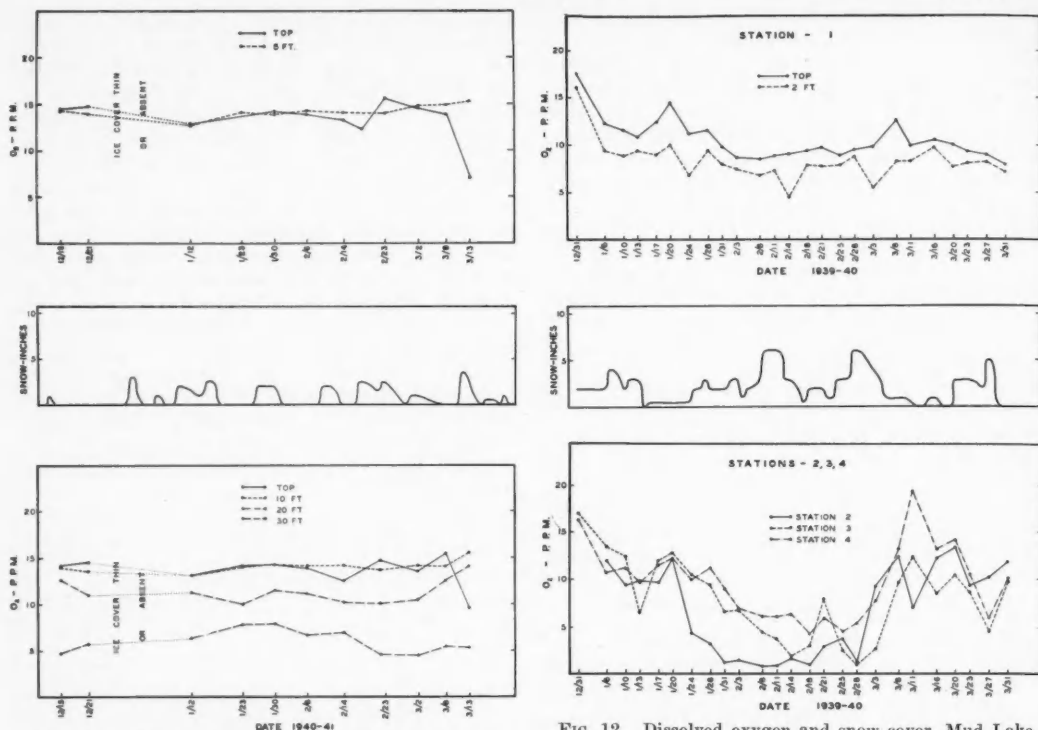


FIG. 11. Dissolved oxygen and snow cover, Clear Lake, 1940-41. Upper curves are for Station 1, lower ones for Station 2a.

cover throughout most of February, and very sharp rises in oxygen in early and mid-March, when the snow was light or absent. These three stations, which initially were chosen on the basis of differences in vegetation and bottom materials, failed to show many significant differences in dissolved oxygen values, the most evident one being that the oxygen at Station 2 (which had a soft marl bottom) for some reason dropped to a low value much sooner than did that at the other stations.

Station 1 was more or less directly in the path of flow of water crossing the lake, and hence its oxygen curves showed less response to changing light conditions, because of the steady influence of the inflowing water. However, it is of interest to note that, in spite of the current, a definite stratification existed at this station, the bottom water always containing less oxygen than the surface water. The inflowing water itself scarcely could have been stratified, since the stream was shallow; therefore even a transitory stay in the deep part of the lake was enough to bring about a distinct stratification.

In 1939-40 the outlet water on Mud Lake almost continuously had less dissolved oxygen than did the inflowing water (Fig. 13). In 1940-41 exactly the reverse condition existed. In other words, during the one winter the water lost oxygen during its stay in

FIG. 12. Dissolved oxygen and snow cover, Mud Lake, 1939-40. The curves for Stations 2, 3, and 4 are for surface samples.

the lake, in the other winter it gained oxygen. It is evident that this difference came about not so much by any shift in the curve for the inlet water from one year to the next, as by a vast change in the curve for the outlet. The correlation with the respective conditions of snow cover and light for the two winters is evident.

Curves are given for only one station in Green Lake (Figs. 14 and 15), since this station fairly well typifies the lake. Here again the relation between surface and bottom water is evident. The curve for the bottom follows closely that for the top, but almost constantly remains below it. This relationship, repeated over and over for various lakes and stations, can lead logically to only one line of reasoning. The two levels of water are subject to the same influences, light on the one hand and oxygen demand on the other, but to different degrees. The bottom water either receives less light and hence produces less oxygen, or is subject to greater oxygen demand and hence loses more oxygen,¹ or both; therefore the oxygen curve for the bottom water falls below that for the surface water. With such a difference, however, the two curves should become progressively

¹ It may be well to take into account the difference in temperature (usually almost 4° C.) between the top and bottom, with perhaps a consequent difference in metabolic activity of the contained organisms.

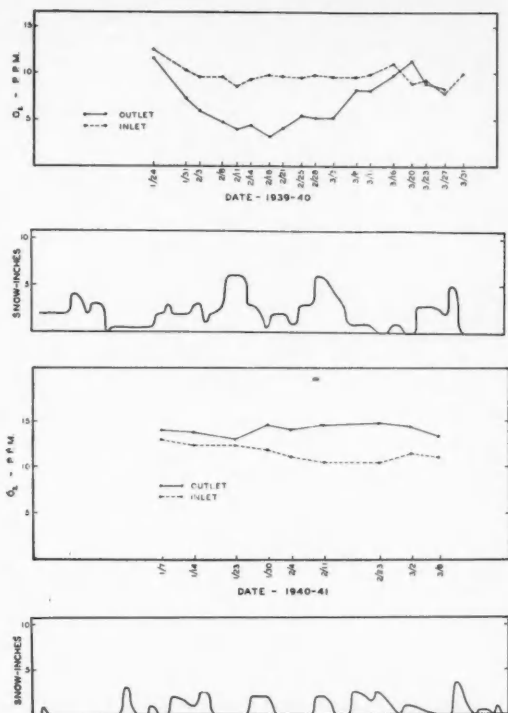


FIG. 13. Dissolved oxygen and snow cover, Mud Lake. Inlet and outlet, 1939-40 and 1940-41. Surface samples.

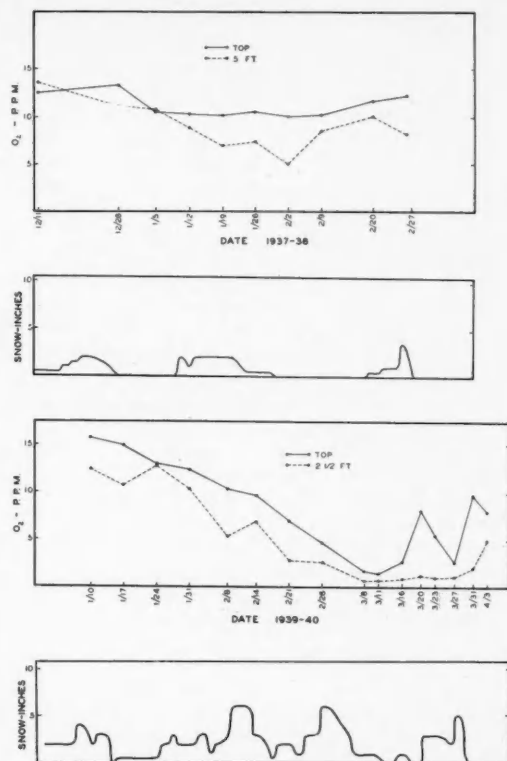


FIG. 14. Dissolved oxygen and snow cover, Green Lake, Station 1, 1937-38 and 1939-40.

more divergent throughout the winter (as in the case of the deeper station in Clear Lake in 1939-40), instead of following each other so closely. For some stations, it seems as if almost as much divergence between the curves exists at the start of the winter as later, and that the curves tend to be roughly parallel. In other words, this is more evidence that stratification may take place, and quite rapidly, even before the ice forms, as is postulated above for the deep station in Clear Lake in 1940-41.

In respect to the amount by which the bottom water at a shallow station may remain lower in oxygen throughout the winter than the surface water, an interesting series is presented in the curves for the several lakes, starting with Clear Lake (Figs. 10 and 11), and progressing through Mud Lake, Green Lake, and Pasinski's Pond (Figs. 12, 14, 15, and 17), to Bog Lake (Fig. 16). In Clear Lake the oxygen was practically the same at the two depths (at Station 1); for Bog Lake the values were widely separated. Yet the tendency, discussed above, for the lower curve to parallel the upper one existed to some extent even in Bog Lake.

Green Lake (Figs. 14 and 15) offers another example of the readily apparent connection between depth of snow on the ice and dissolved oxygen response, in a shallow eutrophic lake. The steady decline of oxygen during the long period of snow cover

in 1939-40 (Fig. 14) contrasts strongly with the almost level (and relatively high) curve for the winter of 1937-38, a winter of comparatively little snowfall. A similar contrast exists between the curves for the two years 1940-41 and 1942-43 (Fig. 15).

The typically dystrophic water of Bog Lake shows, in comparison with the water of the other lakes studied, a set of extremes. In some cases its extreme stratification was almost unbelievable. For example, on January 23, 1941, the oxygen at the surface was 20.2 p.p.m., while at the depth of 5 feet it was 0.0 p.p.m. Most of this difference of 20.2 p.p.m., 16.2 p.p.m. to be exact, occurred between the one-foot level (18.3 p.p.m.) and the two-foot level (2.1 p.p.m.). No doubt such sharp stratification is associated with the brown suspended material of this bog water, and could very seldom if ever be found in a clear-water lake. Also greatly marked is the response of the surface water of Bog Lake (and to a certain extent the water at 1 and 2 feet) to changes in light conditions. This is quite evident in the fluctuations of the oxygen curves for 1939-40 (Fig. 16) in respect to the corresponding changes in the snow-depth curve.

As will be discussed below, under Experimental Studies, it is probable that the data from no one station in Pasinski's Pond can give a very complete

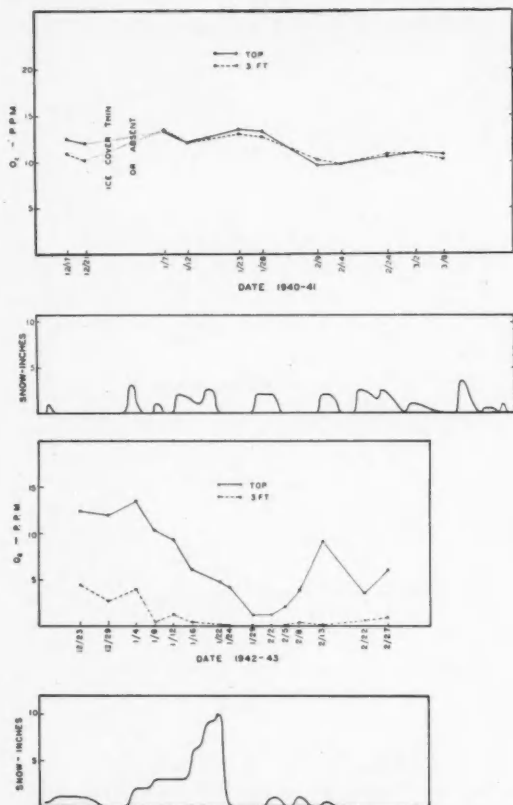


FIG. 15. Dissolved oxygen and snow cover, Green Lake, Station 1, 1940-41 and 1942-43.

picture of conditions in the pond as a whole, since the pond varies so greatly from one part to another. Especially does this qualification pertain to the winter 1939-40. In 1940-41 conditions were somewhat more nearly uniform throughout the pond, and hence may be studied with a fair degree of reliability by the use of one set of curves. Figure 17 gives the oxygen values for Station 26, the deepest station in the pond, for 1940-41. Here it may be noted that, as in the case of other lakes, there is a considerable correspondence in the dissolved oxygen values for the various depths on the same dates. In this instance, however, there are certain deviations from that coordination. The value for the bottom water fluctuated to some extent without respect to that of the surface water, particularly on January 31, when the oxygen at the bottom fell off, while the upper water was gaining oxygen. The extremely high oxygen values at this station throughout most of the winter 1940-41 are indicative of abundant photosynthetic production of oxygen, during a winter of little snow.

The variations in the dissolved oxygen content from one winter to another within the same lake are shown in Figures 18 and 19. The oxygen in the water in

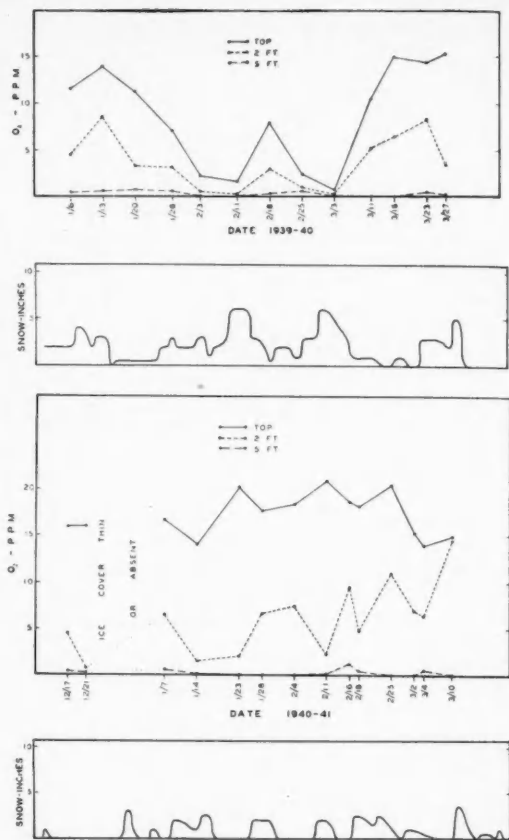


FIG. 16. Dissolved oxygen and snow cover, Bog Lake, 1939-40 and 1940-41.

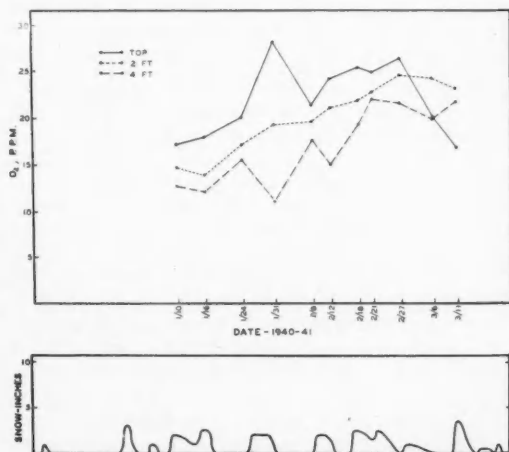


FIG. 17. Dissolved oxygen and snow cover, Pasinski's Pond, Station 26 (south end of pond), 1940-41.

Clear Lake (at the surface) was almost the same in each of three winters, not deviating far from the saturation point most of the time. The evident conclusion is that this water, being only mildly eutrophic, contained not only very little dead organic matter to consume its oxygen, but also very little living phytoplankton to produce oxygen. Hence it simply retained its initial supply of oxygen throughout the winter, with little addition or loss. It became neither excessively low in oxygen during a winter of much snow (1939-40) nor excessively high in oxygen during a winter of little snow (1940-41). Such water

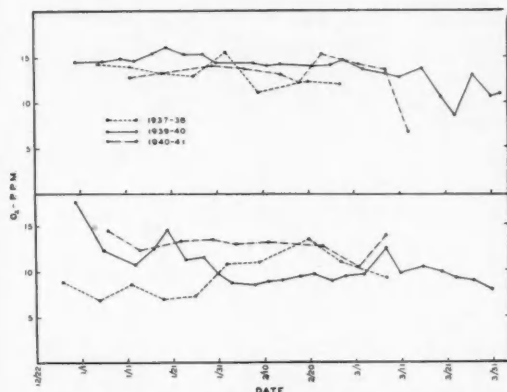


FIG. 18. Dissolved oxygen, different winters compared. Upper, Clear Lake, Station 1, surface. Lower, Mud Lake, Station 1, surface.

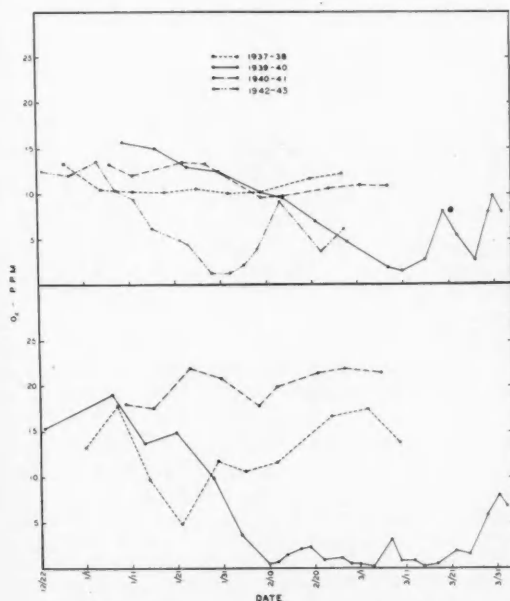


FIG. 19. Dissolved oxygen, different winters compared. Upper, Green Lake, Station 1, surface. Lower, Pasinski's Pond, Station 15 (north end of pond), surface.

probably would be safe from complete oxygen depletion in the longest, most severe winter of the past or future few centuries.

The curves for Mud Lake and Green Lake (especially the latter), however, very plainly show the comparative effects of the different winters on the dissolved oxygen content of the water. The winter of 1939-40 had the most adverse effect, that of 1940-41 the least. The dissolved oxygen in Green Lake diminished rapidly in the early part of the winter of 1942-43, but rose rapidly following the disappearance of the snow cover. The greatest difference, in the examples chosen, is furnished by the curves for Pasinski's Pond, which form an almost perfect spread according to the severity of the different winters.

The vertical distribution of dissolved oxygen for various lakes and for certain selected dates is shown in Figures 20 to 22. In each of these figures the horizontal scale (oxygen) is the same throughout the figure. The vertical scale (depth) varies, in Figure 20, with the lake. This method of diagramming dissolved oxygen is similar to that sometimes used to show the vertical distribution of plankton. Included in Figure 20, for purposes of comparison, are diagrams for Lake Mendota, for certain dates in the winter of 1906-07, the data for which were taken from Birge & Juday (1911).

Changes in vertical distribution of oxygen take place as the winter season progresses. For instance, as mentioned above, the water of Clear Lake was almost uniform, as regards dissolved oxygen content, at all depths at the start of the ice cover in 1939-40. Oxygen at the lower depths gradually decreased, until on March 16 it was very much less than at the surface (correspondingly, the diagram for that date is semi-triangular). A somewhat similar sequence is shown by the diagrams for Lake Mendota, on the same figure, except that the oxygen in Lake Mendota tended to decrease mainly at the bottom, maintaining a somewhat uniform distribution in the upper half of the water. Lake Mendota of course is much deeper than Clear Lake.

However, in Clear Lake in 1940-41, as well as in Green Lake in the same winter, stratification was fairly well developed early in the winter, and the general shape of the oxygen distribution diagram remained somewhat the same throughout the winter. Some rather bizarre figures appear in Figure 20, most of which are occasioned by the somewhat sharp changes in the oxygen of the surface water, such as in Clear Lake on March 13, 1941, when run-in water had appreciably lowered the oxygen in the surface water.

The diagrams for Green Lake, 1942-43 (Fig. 21) depict a steady decrease in dissolved oxygen, first in the bottom water and then at the surface, throughout the early winter. This was followed by pronounced recovery, in the upper water, in the latter half of February.

In Bog Lake, in each of two winters, the oxygen at the bottom was very low even at the start of the

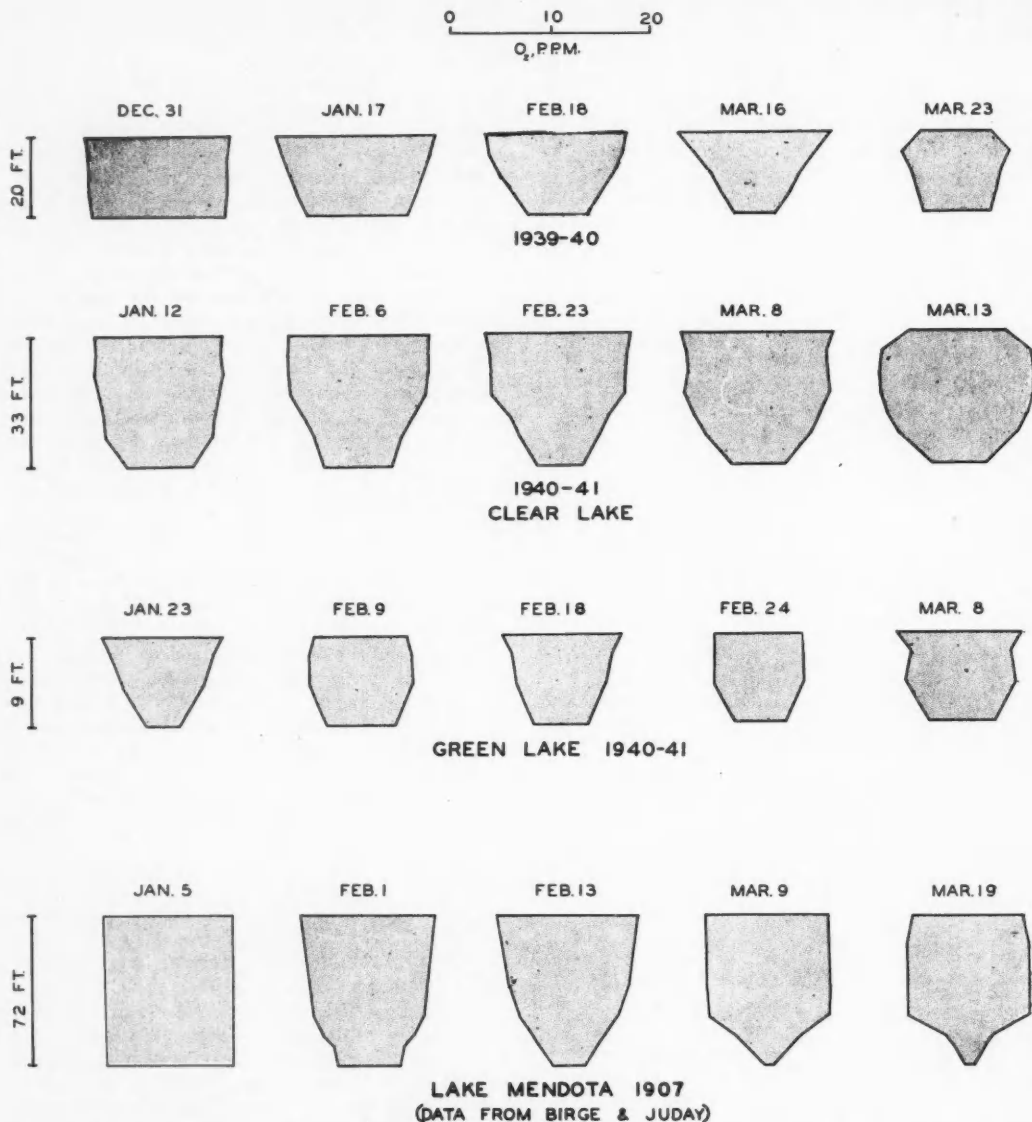
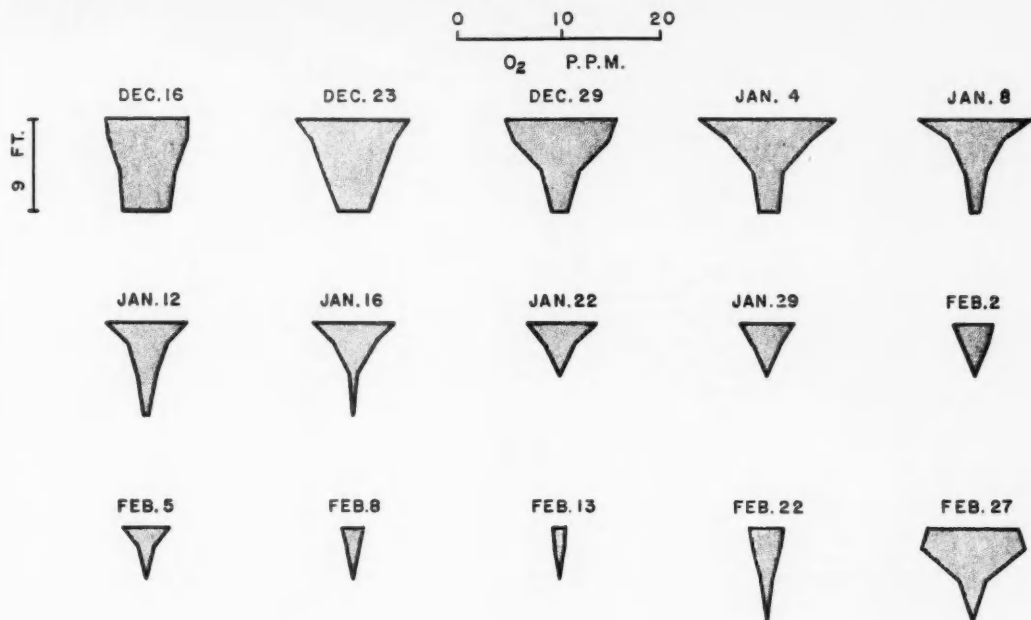


FIG. 20. Dissolved oxygen, vertical distribution. Clear Lake, Green Lake, and Lake Mendota, selected dates. The width of the block diagram at any given depth indicates the amount of oxygen present at that depth.

winter. Here, however, rapid and extreme changes occurred in the amount of oxygen in the upper water, so that the diagrams of Figure 22 vary exceedingly, from the almost perfect triangle for January 30, 1940, to the thin wedge for March 3 of the same winter, to the wine-glass shaped figure for December 21, 1940.

The peak values of dissolved oxygen mentioned above (i.e., 21.0 p.p.m. for Bog Lake and 28.0 p.p.m. for Pasinski's Pond, in 1940-41) are somewhat unusual for ice-covered water, although the literature

has recorded a few similar instances. Griffiths (1936) reported an oxygen content of 22.0 p.p.m. for Long Pool, England, under the ice in February, 1930. In Lake Mendota (Birge & Juday 1911) on March 29, 1906, the upper water contained 12.5 cc. per liter (equal to about 17.0 p.p.m.) of oxygen. Knauth (1899) reported the astoundingly high figure of 49.0 cc. per liter (about 70.0 p.p.m.) in an ice-covered pond which contained very large numbers of algae. There is considerable doubt, however, that his method of dissolved oxygen determination was a reliable one.



1942-43

FIG. 21. Dissolved oxygen, vertical distribution. Green Lake, selected dates, 1942-43. The width of the block diagram at any given depth indicates the amount of oxygen present at that depth.

SPECIAL OBSERVATIONS, GREEN LAKE

FORTY-EIGHT-HOUR OXYGEN VARIATIONS

In order to determine the effects of alternating light and dark periods upon the dissolved oxygen content of the water under the ice, and the possible existence of a diurnal oxygen cycle, a two-day run of sampling was conducted on Green Lake, from January 17 to 19, 1941. Samples were taken at two-hour intervals, starting at 5 P.M. on January 17, and ending at 3 P.M. on January 19.

The oxygen in the surface water remained practically constant throughout the forty-eight hours, the entire range of variation being between 12.3 and 14.3 p.p.m. The slight fluctuations showed no apparent correlation with periods of light and dark.

Much greater changes appeared in the values for the deeper samples. The variation at 5 feet was from a low of 7.2 to a high of 10.5 p.p.m., and 9 feet from 3.4 to 7.6 p.p.m. Again no correlation with daylight and dark was evident.

The situation of greater fluctuation in the deeper water than at the surface is exactly the reverse of that which would be expected if changes in light were the cause of fluctuation, since the upper water is more subject to these changes. The fluctuations in the values for the lower depths were apparently quite at random, and probably are largely explainable by imperfections in the sampling technique (i.e., inability in sampling to strike exactly the same depth

each time), or by shifts in the stratified layers of water.

No well-defined, if indeed any, diurnal variation in oxygen was present. Perhaps this is due to the fact that the processes of photosynthesis and decomposition are considerably slowed down at low temperatures, and hence do not reflect the diurnal changes in light.

This example of course does not prove that diurnal variations in dissolved oxygen under the ice never exist. It may be that at certain times, particularly during periods of unusually high oxygen production (as in Pasinski's Pond in 1940-41), a slight diurnal cycle is present. However, for the average ice-bound lake, it is probable that diurnal variations in oxygen are insignificant.

DISSOLVED OXYGEN, TEMPERATURE, AND ALKALINITY PROFILES

Profile sections of Green Lake, showing isograms of dissolved oxygen, were drawn up for one date in 1940-41 and three dates in 1942-43. Briefly, these profiles were derived as follows. Oxygen determinations were made, at depth intervals of one foot, and at a series of stations at regular horizontal intervals along a line from the mouth of the inlet stream to the dam. This line made a broad curve, roughly following the channel of current, and including Stations 4, 2, 1, and 5 (see Figure 5). The diagrams (Figs. 23-25) are drawn in idealized profile plan, with isograms connecting points of equal dissolved oxygen.

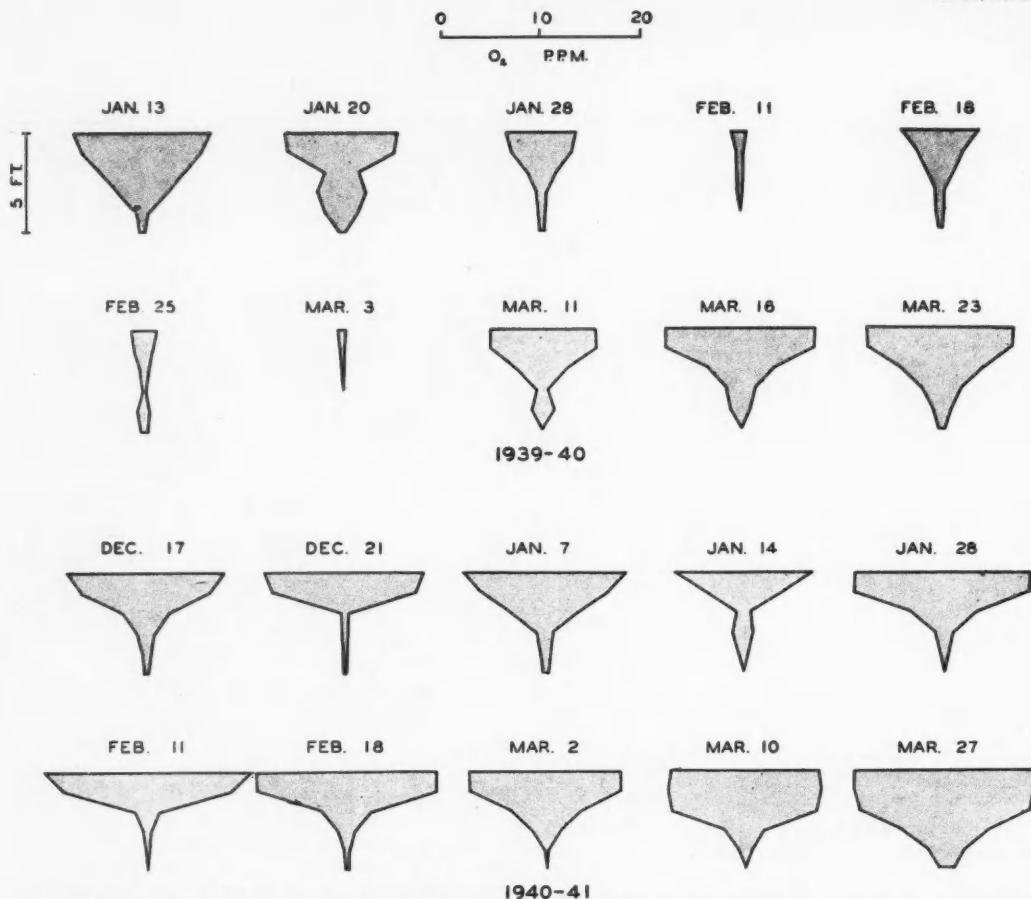


FIG. 22. Dissolved oxygen, vertical distribution. Bog Lake, selected dates, 1939-40 and 1940-41. The width of the block diagram at any given depth indicates the amount of oxygen present at that depth.

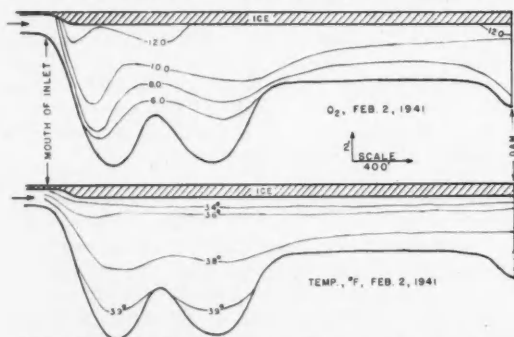


FIG. 23. Dissolved oxygen and temperature profiles, Green Lake, February 2, 1941. See text for description.

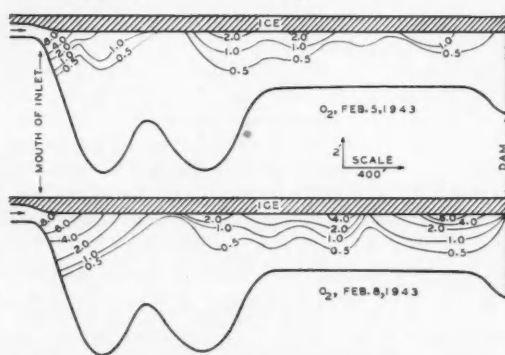


FIG. 24. Dissolved oxygen profiles, Green Lake. Upper, February 5, 1943. Lower, February 8, 1943. See text for description.

The vertical scale is greatly exaggerated with reference to the horizontal scale.

A similar diagram showing isothermal lines, and another with isograms of methyl orange alkalinity (each for one date only) were constructed (Figs. 23 and 25).

As shown by the diagrams, the dissolved stratification is sharpest near the bottom, and the oxygen isograms tend to follow the bottom contour. On the other hand, the temperature changes most rapidly

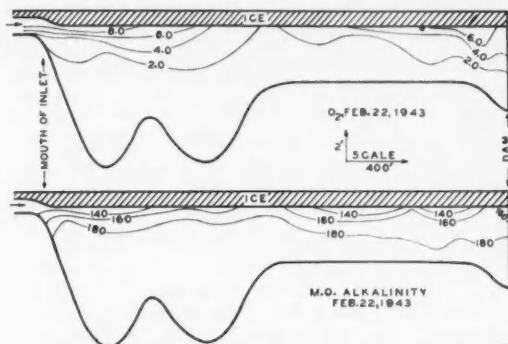


FIG. 25. Dissolved oxygen and methyl orange alkalinity profiles, Green Lake, February 22, 1943. See text for description.

immediately under the ice, and the isotherms tend to be parallel to the surface contour.

The profile of February 2, 1941, represents the lake at a time of relatively high dissolved oxygen; those of the three dates in 1943 show comparatively low oxygen. On February 5, 1943, only a small part of the area of the transect had an oxygen value of 2.0 p.p.m. or more, and by far the largest part had less than 0.5 p.p.m. The inflowing water, however, was carrying over 8 p.p.m. at this time. The amount of oxygen enrichment which thus far had been brought about by this means is evident from the diagram. It must be remembered, of course, that the diagram represents a section along the channel; the effect of the inlet upon the lake as a whole is not nearly so great.

The oxygen along the profile had increased noticeably by February 8, chiefly as a result of rains and thaws. That this increase came from the surface is well indicated in the diagram, which shows a vertical shift in the isograms. However, in spite of this shift, the same general pattern was carried over from the one date to the other. During the three-day interval a large amount of water, relatively high in oxygen, was brought in by the inlet stream; its effect is displayed in the changed pattern of the isograms at that end of the section.

By February 22, a considerable amount of oxygen had been added to the upper water, by inflowing water (possibly also to some extent by photosynthesis), almost completely obliterating the former pattern of the profile. A few vestiges of that pattern remained, however, particularly the "low" point at about 1,500 feet from the mouth of the inlet. The local effect of water from the inlet stream had largely been absorbed by, even as it contributed to, the general increase in oxygen in the upper layers of water.

Evidence that much of the change was caused by inflowing water is given by the diagram for methyl orange alkalinity, for the same date (February 22). The alkalinity isograms tended somewhat to follow those for oxygen. The normal situation toward the end of winter stagnation is for the alkalinity to be

greatest at the bottom, and least just under the ice. But without the entrance of relatively soft water (from surface or other inflow), the alkalinity at the surface in Green Lake usually does not fall below 175 p.p.m. The values, shown on the diagram, of 140 p.p.m. or less, definitely are attributable to inflowing water.

An index, by means of which the relative average amounts of oxygen represented on the four dissolved oxygen profile diagrams may be compared, has been derived as follows. For each diagram, the area between each two consecutive isograms was measured, and computed in terms of percent of the total area of the diagram. This figure then was multiplied by the mean oxygen value of the two isograms. These products were totalled, and their sum divided by the total area (i.e., by 100 percent). The quotient was assumed to represent the average value for the entire diagram, and thus for that transverse section of the lake at the time.

How reliably this index may be applied to the lake as a whole is not known, for of course only one section is represented, and that a rather special one (along the channel). However, it surely is a much better index that one obtained from only a single station; and it at least gives a general idea of the condition of the entire lake.

These calculated mean values were:

Feb. 2, 1941	9.3 p.p.m.
Feb. 5, 1943	0.6 p.p.m.
Feb. 8, 1943	1.0 p.p.m.
Feb. 22, 1943	2.1 p.p.m.

These figures show something of the increase (mentioned above) of oxygen during February, 1943. They also point out that which is not instantly apparent in the diagrams, that is, that as concerns the section as a whole the increase in oxygen was not numerically great, even though the water near the surface did become much enriched in oxygen. A lake may show apparently great recovery from low oxygen conditions, when judged by one or a few surface samples, and yet continue to be relatively low in average oxygen content. In fact, it often is the case, in the average eutrophic lake in this region, that the oxygen near the bottom diminishes quickly after the lake becomes ice-covered, and remains low throughout the winter; thus the shifting back and forth between high and low oxygen values occurs only in the water near the surface. In effect, a "squeezing-out" is accomplished; that is, the fish presumably are confined, for a large part of the winter, to a more or less thin layer of water immediately under the ice.

PH, CARBON DIOXIDE, ALKALINITY

A fairly complete set of observations were made of pH, methyl orange alkalinity, and (particularly in 1940-41) free carbon dioxide. These figures are not presented here in tabular form, since they are largely repetitions.

Except for the occasional influence of melted snow or ice, or rain, on surface samples, the pH in any particular lake tended to change little throughout a winter. All of the lakes studied, except Bog Lake, had water of comparatively high buffering capacity, and the pH usually remained reasonably close to the figure pH 8.0, dropping below 7.0 only at times of serious decomposition.

Even the water of Bog Lake, with its extremely low bicarbonate content, showed a fluctuation, around the value pH 6.0, of only about 1.0 pH unit.

Likewise, significantly large quantities of titratable ("free") CO_2 were seldom found. Even at times of oxygen depletion, the hard-water lakes showed only a few p.p.m. of free carbon dioxide. Bog Lake, with its soft, acid water, always contained titratable acidity (probably caused by other acids in conjunction with carbonic acid), but usually in amounts of less than 30 p.p.m.

In general, the condition of the water, as regards the welfare of aquatic organisms in the winter, is described more forcefully and understandably by dissolved oxygen data and graphs than by the figures for alkalinity and CO_2 . A few general observations regarding the alkalinity values are in order, however.

As might be expected, free CO_2 and pH are fairly closely correlated with dissolved oxygen. The same processes of decay which use oxygen produce carbon dioxide, and hence lower the pH. Conversely, the photosynthetic production of oxygen uses up carbon dioxide and raises the pH. To a certain degree, therefore, CO_2 or pH could furnish a rough index to conditions under the ice, especially if the usual or normal values were known. However, certain complications, some of which are unforeseen, may arise.

The pH sometimes is influenced (in bog lakes especially) by acids other than carbon dioxide. Inflowing water, from melted snow and ice, may greatly alter (lower) the buffering power of the water, and hence affect pH (see Figure 26).

The physiological significance of free carbon dioxide is discussed briefly below in the section on winter suffocation.

Under the influence of developing stagnation, the so-called total alkalinity, or alkalinity to methyl orange, gradually increases by a relatively small amount. With conditions of stratification, the water near the bottom usually has a higher methyl orange alkalinity than that near the surface. Figure 26 (for Clear Lake, 1939-40) shows this difference, as well as the tendency for the curves representing the alkalinity at various depths to spread apart as the winter progresses, after starting at almost the same value. This behaviour is somewhat comparable to that of the dissolved oxygen curves for the same station. The sharp fluctuations and extremely low alkalinity values shown by the curve of the surface were caused by dilution with rain or melted snow or ice.

BIOCHEMICAL OXYGEN DEMAND

The biochemical oxygen demand (abbreviated B.O.D.) is the oxygen consumed, by bacterial action,² in a certain period of time, from a sample incubated in the dark at a fixed temperature. Conventionally, if the limiting conditions are not indicated, it is understood that the time period is five days (120 hours) and the incubation temperature 20°C . In the present series of B.O.D. determinations a considerable number of samples were incubated at 0°C ., and some of these had an extended incubation up to 60 days.

B.O.D. gives a rather accurate picture of the relative organic richness of a water sample, and the likelihood of the depletion of its dissolved oxygen supply in a given time. When measured at 0°C ., the B.O.D. of a sample of water from an ice-covered lake provides a rough indication of the probable behaviour of that water with respect to oxygen depletion.

The B.O.D. data obtained are summarized in Tables 3-5. As mentioned above, in the section on Methods, the values given in these tables usually are weighted means of two or more samples, set up at different dilutions. Table 3 gives the B.O.D. values for five-day incubation at 20° , and Table 4 those for five days at 0° . Table 5 is for the 60-day B.O.D. run at 0° .

Certain facts are apparent. The B.O.D. of the water in Clear Lake was very much less than that of the more eutrophic waters. Extremely high B.O.D. was found for many samples from Bog Lake and Pasinski's Pond. The B.O.D. at 0°C ., for nearly all of the waters studied, showed a correlation with that at 20° . The values for 0° averaged on the order of four-tenths of those for 20° .

²Theoretically only bacterial action (and possibly that of algae, protozoa, and microscopic metazoa) is involved. Actually a part of the demand (usually a small part) may come from purely chemical oxidation.

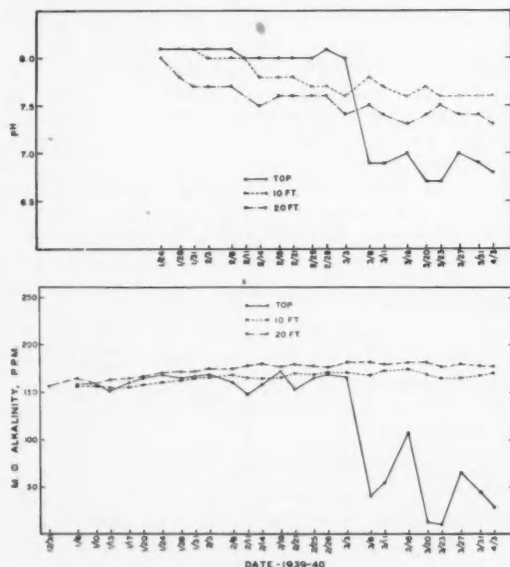


FIG. 26. Methyl orange alkalinity (lower) and pH (upper). Clear Lake, Station 2, 1939-40.

TABLE 3. Biochemical oxygen demand (B.O.D.), five days at 20° C. Samples from various lakes, 1940-41. Data expressed in p.p.m.

Lake	Station number	Depth	Dates							
			12/21	1/7	1/23	1/28	2/9	2/18	3/11	
Green	1	Surface	2.9	2.0	...	3.0	2.3	
		Bottom	1.7	2.4	...	2.3	1.8	
	2	Surface	1.5	1.9	1.9	3.8	1.5	2.0	...	
		2 feet	1.6	2.0	2.1	...	2.0	
		5 feet	2.0	2.6	0.3	2.6	2.1	2.2	...	
		9 feet	0.0	1.9	3.0	1.9	1.1	2.1	...	
	3	Surface	3.2	3.1	...	3.3	2.4	
		Bottom	2.7	2.9	...	3.9	3.2	
	4	Surface	2.9	1.8	...	2.8	3.3	
		4 feet	2.2	
		8 feet	2.3	0.8	...	0.0	3.1	
	5	Surface	...	3.1	...	2.6	1.4	
		Bottom	...	2.9	...	2.9	1.8	
	Inlet		2.0	0.0	1.5	0.8	1.0	
	Outlet		1.7	4.0	...	2.7	2.5	
Mud	1	Surface	2.1	3.1	1.4	2.6	3.7	2.6	3.9	
		Bottom	1.3	2.2	1.4	1.9	2.2	2.1	2.4	
	Inlet		2.1	2.1	2.7	2.0	2.2	1.5	1.3	
			2.1	2.1	2.6	2.3	4.3	2.4	2.6	
	Outlet		
			
Clear	1	Surface	...	1.2	...	3.8	2.9	1.6	...	
		Bottom	...	0.5	1.8	1.7	2.1	...	1.2	
	2a	Surface	2.3	0.8	2.2	4.3	3.2	
		5 feet	...	0.6	1.5	2.4	1.8	
		10 feet	1.5	0.8	1.6	3.6	2.3	
		15 feet	...	0.6	1.7	1.8	1.0	
		20 feet	1.6	0.0	2.8	1.2	1.9	
		25 feet	...	0.0	1.4	0.9	1.3	
		33 feet	0.0	0.0	0.0	0.0	0.0	
			
			
			
			
			
Bog		Surface	13.4	15.2	9.8	10.0	13.2	8.8	12.0	22.0+
		1 foot	8.4	8.2	5.2	18.3	7.3	8.4
		2 feet	1.4	5.6	2.2	5.1	7.0+	2.0+	4.2	7.2
		3 feet	1.8	1.8	4.0	3.9	5.6	3.0
		4 feet	2.2	3.6	2.8	4.6	3.8	3.8
		5 feet	2.2	2.6	3.4	4.2	4.2	3.4	6.2	2.9
		
		
Pasinski's Pond	15	Surface	3.0	15.0	42.0	10.6	14.7	6.8	12.0	...
		Bottom	1.3	2.5	5.7	11.2	2.6	5.7	2.7	...
	24	Surface	...	7.6	6.2	5.2	10.0	11.0	20.2	...
		Bottom	...	1.1	5.5	4.8	4.0	5.9	7.9	...
	26	Surface	4.2	11.5	11.0	2.8	8.3	2.5	36.3	6.4
		1 foot	...	4.4	4.5	2.4	9.2	9.4	34.3	...
		2 feet	...	4.2	3.1	6.1	5.3	7.6	20.1	10.0
		3 feet	...	4.0	2.8	5.8	2.6	11.0	15.7	...
		4 feet	1.5	1.7	4.9	4.4	1.4	10.9	6.1	7.5
		5 feet
	27	Surface	12.9	7.1	4.3	21.8	4.8	24.2
		Bottom	...	4.7	0.0	3.4	5.2	6.3	3.6	...
	20	Surface	...	6.7	9.1	10.1	10.0	8.1	20.6	...
		Bottom	...	3.2	0.0	4.8	3.6	5.2	3.2	...

Worthy of note is the regularity with which the B.O.D. at any particular station was higher in the upper water than near the bottom. Sometimes the differences were very large, such as that between 24.2 p.p.m. and 3.6 p.p.m., at Pasinski's Pond, Station 27, February 12, 1941. This sharp decline of B.O.D.

TABLE 4. Biochemical oxygen demand (B.O.D.), five days at 0° C. Samples from various lakes, 1941. Data expressed in p.p.m.

Lake	Station number	Depth	Dates			
			2/9	2/18	3/11	
Green	1	Surface	0.6	
		Bottom	0.8	
	2	Surface	0.7	0.0	...	
		2 feet	1.3	...	0.5	
		5 feet	0.8	0.3	...	
		9 feet	0.0	0.4	...	
	3	Surface	1.2	
		Bottom	1.8	
	4	Surface	0.6	
		Bottom	3.3	
	5	Surface	0.5	
		Bottom	0.6	
	Inlet		0.6	
	Outlet		0.9	
Mud	1	Surface	0.5	1.2	...	
		Bottom	0.6	1.4	...	
	Inlet		0.0	0.6	...	
			1.0	1.3	...	
	Outlet		
			
Clear	1	Surface	0.0	0.0	...	
		Bottom	0.5	...	0.0	
	2a	Surface	0.0	
		5 feet	0.4	
		10 feet	0.4	
		15 feet	0.0	
		20 feet	0.3	
		25 feet	0.7	
		33 feet	0.0	
			
			
			
Bog		Surface	3.9	4.1	2.4	9.4
		1 foot	1.1	6.1
		2 feet	5.4	1.4	1.2	2.8
		3 feet	0.0	0.0
		4 feet	0.0	0.0
		5 feet	0.0	0.0	1.0	1.4
		
		
Pasinski's Pond	15	Surface	1.1	5.7
		Bottom	3.0	1.9
	20	Surface	2.7	7.8
		Bottom	2.8	0.5
	24	Surface	3.4	9.4
		Bottom	3.9	8.4
	26	Surface	0.0	16.1	1.1	22.7
		1 foot	0.0	15.3
		2 feet	3.0	7.5	2.8	4.0
		3 feet	2.8	5.8
	27	4 feet	2.5	2.9	2.5	2.2
		Surface	4.1	11.8
		Bottom	4.1	1.9
		
		
		
		
		

with increasing depth probably indicates a greater accumulation of suspended organic materials, such as zooplankton and phytoplankton, in the surface waters. Given the right conditions of darkness, and so forth, as in a B.O.D. sample bottle, this material decomposes rather rapidly, giving a high B.O.D. figure.

TABLE 5. Biochemical oxygen demand (B.O.D.), 60 days at 0° C. Samples taken March 11, 1941. Data expressed in p.p.m.

Lake	Station	Depth	Days	B.O.D., p.p.m.	Lake	Station	Depth	Days	B.O.D., p.p.m.
Clear	1	3 feet	5	0.0	Green	2	3 feet	5	0.5
			10	1.6				10	1.7
			15	2.1				15	1.8
			20	1.3				20	1.8
			30	0.2				30	2.2
			40	2.8				40	7.0
			50	1.9				50	5.4
			60	2.6				60	5.4
Eog	Surface		5	9.4	Pasinski's Pond	26	Surface	5	22.5
			10	20.0				10	29.6
			15	27.6					
			20	31.6					
	2 feet		5	2.8			2 feet	5	4.0
			10	4.9				10	4.0
			15	5.4				15	7.4
			20	6.5				20	9.5
			30	8.3				30	15.2
	4 feet		40	9.5			4 feet	40	18.4
			40	15.4				50	18.0
			50	...					
			60	20.4					
	5 feet		5	1.4				5	2.2
			10	4.4				10	4.3
			15	5.2				15	5.2
			20	5.8				20	5.0
			30	8.8				30	6.9
			40	10.8				40	6.7
			50	7.6				50	6.7
								50	11.6

In the water under the ice, this suspended organic matter settles slowly, probably being oxidized as it sinks. Hence its power of utilizing oxygen is diminished by the time it reaches the lower water.

Opposed to this reasoning stands the fact that the upper water usually maintains, throughout the winter, much more oxygen than does the bottom water. This difference, however, can at least in part be accounted for by the much greater production of oxygen in the upper water.

The high B.O.D. values obtained for certain samples (Tables 3 and 4) indicate water exceedingly rich in organic material. Many samples from Pasinski's Pond had a 5-day demand, at 20°, of over 25 p.p.m., with a high of 42.0 p.p.m. These values are even higher than those of some badly polluted waters. For instance, in the waters of Green Bay (Williamson et al. 1939), which were subject to sulfite pulp mill pollution, most of the samples taken had a 5-day B.O.D. of 10 p.p.m. or less; and even in the extremely putrid waters of East River values higher than 25 p.p.m. were very seldom encountered.

Figure 27 shows the B.O.D. at 0° C., over an extended period of time, of three samples from Station 26, Pasinski's Pond, and one sample from Clear Lake (the samples were taken on March 11, 1941). The curves as drawn are somewhat idealized, because too few data are at hand to make sure the exact shape of the curves. However, they are of the same shape as B.O.D. curves in general.

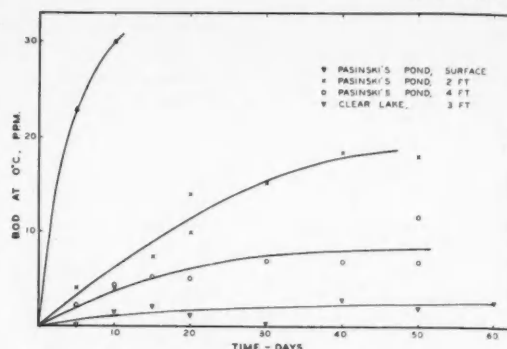


FIG. 27. Biochemical oxygen demand at 0° C. Samples taken March 11, 1941.

The curves for the three depths in Pasinski's Pond exhibit a remarkable spread, and also quite a contrast to the almost flat curve for Clear Lake. The water at the surface in Pasinski's Pond had approximately nine times as much B.O.D. in five days (22.5 p.p.m.) as did that in Clear Lake in sixty days (2.6 p.p.m.). Such comparative figures go far toward explaining why Pasinski's Pond can lose nearly all of its dissolved oxygen within a few days, while Clear Lake almost invariably retains oxygen nearly to the saturation point throughout the entire winter.

LIGHT PENETRATION

During the winters of 1940-41 and 1942-43, a considerable number of measurements were made of the transmission of light through water, ice, and snow, in the various situations which obtained at the lakes which were being investigated. The photometer used, and the methods employed, are described above. In order to utilize deeper snow than was available on the lakes in the Ann Arbor region, visits were made to certain lakes in Iosco and Montmorency counties, Michigan. The light transmission data are summarized in Tables 6-9.

Considerable information may be obtained from the literature. Numerous papers have been written concerning light penetration into water, both sea water and that of lakes. Among the many investigators who have done work on this subject, there may be mentioned Clarke, Shelford, Poole & Atkins, Utterback, Birge & Juday, and Pearsall & Ulliyott, most of whom are cited below. Although much less work has been done on snow and ice, a few informative papers have appeared.

TRANSMISSION THROUGH WATER

The characteristics of various waters with respect to the transmission of light have been reviewed by Welch (1935, pp. 72-79), Birge & Juday (1929), and more recently by Clarke (1939) and by Utterback (1941), and therefore are only briefly mentioned here. The observations of this study agree, in general, with the conclusions of these various writers.

It is well known that even the clearest waters impede the passage of light to a certain extent. Light

TABLE 6. Light transmission through water, ice, and snow. Field measurements at certain lakes, 1941. Results expressed in foot-candles incident on photometer target, and in percentage transmission.

Date, 1941	ICE		SNOW		Depth ¹	Intensity, foot-candles	PERCENTAGE TRANSMISSION								
	Thick-ness, inches	Condi-tion	Thick-ness, inches	Condi-tion			No filter	Red	Green	Blue					
CLEAR LAKE															
Feb. 23	7½	Clear	None	Air	8000					
					Ice	6700	84					
					1'	5400	68					
					2'	4560	57					
					3'	3800	48					
					6'	1920	24					
					9'	1360	17					
					12'	820	10.2					
					15'	580	7.2					
					18'	400	5.0					
					21'	300	3.8					
					24'	206	2.6					
					27'	142	1.8					
	30'	112	1.4									
	7	Clear	¾-1	Dry, light	Air	7300					
					Ice	182	2.5					
					(Same)	(Snow removed)	Air	7000			
				Ice	3800	54						
Mar. 13	6	—	None	Air	4800					
					Ice	2540	53	53	53	54					
					3'	1400	29	27	32	28					
					6'	1000	21	16	23	13					
					9'	690	14.4	9.8	16	7.4					
					12'	490	10.2	6.0	12	4.0					
					15'	340	7.1	4.0	8.7	2.4					
					18'	250	5.2	2.6	6.6	1.5					
					21'	188	3.9	1.7	5.0	0.9					
					24'	138	2.9	1.2	3.7	0.5					
					27'	100	2.1	0.8	2.8	0.3					
					30'	76	1.6	0.5	2.2	0.2					
					32'	55	1.1	0.4	1.6	0.2					
					GREEN LAKE										
					Mar. 13	5	Fairly clear	None	Air	2120
Ice	1250	59	57	59						58					
MUD LAKE															
Feb. 23	8½	Clear	None	Air	3200					
					Ice	2150	67					
	7½	Partly cloudy	None	Air	3700					
					Ice	820	22					
	10¼	Very cloudy	None	Air	4700					
					Ice	340	7.2					
	6½	Clear	2-2½	Crusted	Air	5550					
					Ice	55	1.0					
	(Same)	(Snow removed)	Air	5900							
			Ice	3100	53							
BOG LAKE															
Feb. 25	9½	Milky	1-¾	Dry, light	Air	9200					
					Ice	106	1.15					
	(Same)	(Snow removed)	Air	9300							
			Ice	1340	14.4							
	9½	Milky	1¾	Dry	Air	9440					
					Ice	154	1.63					
					2'	100	1.06					
					3'	27	0.29					
					4'	12.4	0.13					
					5'	7.0	0.07					

TABLE 6 (continued)

Date, 1941	ICE		SNOW		Depth ¹	Intensity, foot-candles	PERCENTAGE TRANSMISSION			
	Thickness, inches	Condition	Thickness, inches	Condition			No filter	Red	Green	Blue
Mar. 13	10	Soft on top	1	Slushy	Air	3450
					Ice	138	4.0	4.5	4.0	2.5
					13"					0.19
					15"					0.19
					24"	17	0.49	1.14	0.42	...
	(Same)		(Snow removed)		Air	2500
					Ice	340	13.6	15.8	14.4	8.3
					13"					2.1
					16"					0.46
					24"	50	2.0	3.0	1.9	0.02
SOUTH LONDO LAKE										
Mar. 5	24	Partly cloudy	10	Dry	Air	7600
					Ice	4.0	0.05			
	(Same)		(Snow removed)		Air	7600
					Ice	580	7.6			
EAST FISH LAKE										
Mar. 20	14	Partly cloudy	5	Dry	Air	4650
					Ice	10.5	0.23	0.21	0.30	0.23
					3'	10.5	0.23			
					6'	9.0	0.19	0.13	0.24	0.15
					9'	7.2	0.15	0.09	0.18	0.09
					12'	5.5	0.12	0.07	0.14	0.07
					15'	4.5	0.10	0.05	0.11	0.06
					18'	3.8	0.08	0.04	0.10	0.04
					21'	3.2	0.07	0.03	0.07	0.04
					24'	2.7	0.06	0.03	0.06	0.03
					27'	2.2	0.05	0.02	0.05	0.03
					30'	1.6	0.03	0.02	0.04	0.02
	(Same)		(Snow removed)		Air	4650
					Ice	470	9.5	9.3	10.8	7.4
MIDDLE FISH LAKE										
Mar. 21	16	Fairly clear	6	Crusted	Air	9900
					Ice	9.3	0.09	0.10	0.11	0.05
					19"	8.5	0.09	0.10	0.11	0.05
					22"	7.8	0.08	0.09	0.10	0.04
					28"	7.2	0.07	0.09	0.10	0.03
	(Same)		(Snow removed)		Air	10600
					Ice	1220	11.5	11.3	12.2	8.1
					19"	1020	9.6	10.1	11.5	5.7
					22"	930	8.8	8.8	10.2	3.6
					28"	720	6.8	7.1	7.5	1.9
WEST FISH LAKE										
Mar. 21	16	Fairly clear	6½	Crusted	Air	10400
					Ice	9.4	0.09	0.07	0.13	0.12
					2'	8.7	0.08	0.07		0.11
					3'	7.5	0.07	0.03		0.06
					4'	6.8	0.07	0.05		0.04
					5'	6.2	0.06	0.05	0.10	0.03
					6'	6.0	0.06	0.04	0.08	0.02
					7'	5.2	0.05	0.04	0.05	0.01
					8'	4.2	0.04	0.03	0.06	0.01

¹Below upper surface of ice.

(in the yellow-green region of the spectrum) is reduced by passing through 100 meters of distilled water, to between 1 and 2 percent of its incident value (Clarke 1939). Natural waters vary from those almost as clear as distilled water, to the highly colored waters of bog lakes or the extremely turbid waters of silt-laden streams, in which the light may

TABLE 7. Light transmission through ice. Field measurements at certain lakes.

Lake	Date	ICE		PERCENTAGE TRANSMISSION			
		Thick- ness, inches	Condition	No filter	Red	Green	Blue
Clear.....	2/23/41	7½	Clear	84
Mud.....	2/23/41	8½	Clear	67
Green.....	3/13/41	5	Fairly clear	59	57	59	58
Clear.....	2/23/41	7	Clear	54
Mud.....	2/23/41	6½	Clear	53
Clear.....	3/13/41	6	Fairly clear	53	53	53	54
Mud.....	2/23/41	7½	Partly Cloudy	22
Bog.....	3/13/41	10	Soft on top	14	16	14	8.3
Bog.....	2/25/41	9½	Milky	14
Green.....	2/ 8/43	15	Cloudy on top	11.6	12.4	12.6	7.2
M. Fish.....	3/21/41	16	Fairly clear	11.5	11.3	12.2	8.1
E. Fish.....	3/20/41	14	Partly cloudy	9.5	9.3	10.8	7.4
Green.....	2/ 8/43	15	Cloudy on top	8.7
S. Londo.....	3/ 5/41	24	Partly cloudy	7.6
Mud.....	2/23/41	10½	Very cloudy	7.2
Green.....	2/ 2/43	15	Cloudy on top	2.0	2.4	2.1	1.0

TABLE 8. Light transmission through snow. Field measurements at certain of the lakes studied. Percentage transmission obtained by calculation (see text).

Lake	Date	SNOW		PERCENTAGE TRANSMISSION			
		Thick- ness, inches	Condition	No filter	Red	Green	Blue
Bog.....	3/13/41	1	Slushy	29	28	28	30
Green.....	2/ 2/43	1	Crusted	17	17	23	18
Green.....	2/ 8/43	1	Crusted	13
Green.....	2/ 8/43	1	Crusted	10.4	10.0	9.3	9.3
Bog.....	2/25/41	17½	Dry, light	8.0
Clear.....	2/23/41	7½ - 1	Dry, light	4.6
E. Fish.....	3/20/41	5	Dry	2.5	1.9	2.5	2.4
Mud.....	2/23/41	2 - 2½	Crusted	1.9
M. Fish.....	3/21/41	6	Crusted	0.8	0.9	0.9	0.6
S. Londo.....	3/ 5/41	10	Dry	0.7

TABLE 9. Light transmission through snow, laboratory experiments, 1941. The source of light was an incandescent bulb.

Date, 1941	Snow Condition	Depth, inches	PERCENTAGE TRANSMISSION			
			No filter	Red	Green	Blue
Feb. 22...	Somewhat wet...	½	13
		1	1.1
		2	0.54
Mar. 23...	Fairly dry; lumpy.	4	tr.
		1	3.4
		2	1.1
Mar. 23...	Dry; screened....	3	0.21
		4	tr.
		1	5.6	2.5	3.3	4.0
		2	0.81	1.1	0.72	tr.
		3	0.04	0.15	0.14	0.0
		4	tr.	tr.	tr.	0.0

be reduced to a fraction of 1 percent at depth of one meter.

It has been demonstrated that, as a rule, the diminu-

tion of the intensity of light in its passage through water follows a definite mathematical formula, the relationship between the depth of water and the amount of light penetrating to that depth being such that it may be plotted as a straight line on semi-logarithmic paper³ (Clarke 1939, p. 27). The slope of that line is an index of the relative transparency of the water. Many examples of this relationship have been presented by Clarke, by Birge & Juday (1929), Utterback (1941), and others.

The penetration of light through the ice-covered waters of some of the lakes of this study is plotted in this manner in Figure 28 (this figure is explained more fully below). Quite evident are the comparative rapidity with which the colored water of Bog Lake absorbed light, the moderately good transmission through the rather clear waters of Clear and East Fish Lakes, and the extremely low absorption of light in the water of Crater Lake (data from Utterback et al. 1942).

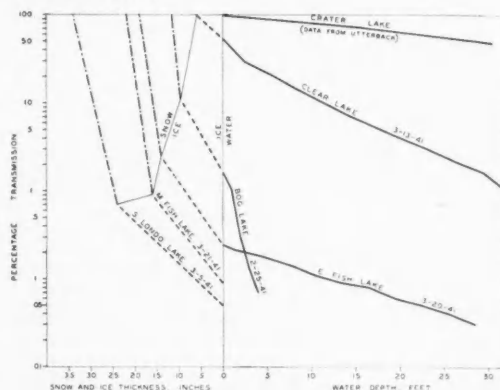


Fig. 28. Percentage transmission of light through snow, ice, and water. Various lakes. See text for explanation of diagram.

As indicated in the papers cited above, there are very large differences in the relative transmission, through water, of light of different spectral qualities. These differences depend in kind and amount upon the type of water. In distilled water, or other very clear water, such as that of the Sargasso Sea, penetration is best effected (within the range of visible light) by blue light, and progressively less well by green, yellow, and red light.

In slightly less clear water, such as that of the clearest inland lakes in Michigan, light in the green or yellow-green portion of the spectrum is transmitted in the greatest amount, red light in the least, and blue light to an intermediate extent. In moderately clear lakes, penetration is greatest in the yellow-green, and considerably less in both the red and the blue. As shown in Figure 29, the water of East Fish Lake was found to have these characteristics.

³In many lakes, however, certain conditions, such as differences in the amount of suspended material at various depths, may cause more or less irregular variations in the transparency of the different layers of water (see Whitney 1938, Chandler 1942, and others).

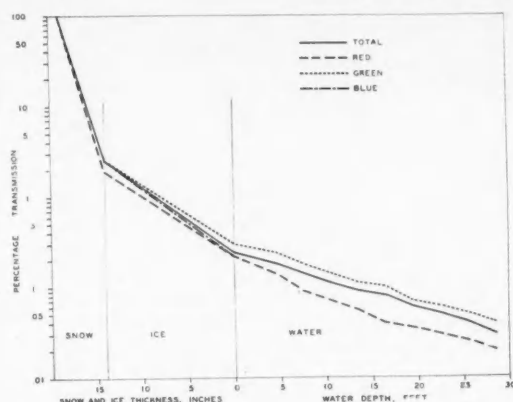


FIG. 29. Percentage transmission of light of different wave lengths through snow, ice, and water. East Fish Lake, March 20, 1941. "Total" light is diffuse daylight as recorded by a Weston cell.

In the less transparent waters there is a shift toward greater relative penetration in the longer wave lengths (yellow, orange, and red), and in waters of very low transparency, such as highly colored bog waters, the transmission of red light is many times as great as that of green light, and blue light is almost entirely excluded. This differential penetration in colored water is illustrated by Figure 30, which shows the relative spectral transmission through the water of Bog Lake. It is probable that the relatively slight ability of light of the shorter wave lengths to penetrate bog water depends in some way on the presence of suspended particles, since water which is turbid because of suspended silt exhibits the same property (Higgins 1932, p. 523).

In addition to the loss of light in the water itself, there is, in open water, a surface loss, sometimes amounting to a considerable portion of the total light. According to Clarke (1939), only a small part of this loss actually is due to reflection; the remainder is caused by a proportionately high rate of extinction in the uppermost layer of water.

Since all of the observations of the present study pertained to water which was covered with ice, it is difficult to assign any value for "surface loss." In making a measurement of the light penetration through the ice, the target of the photometer was held tightly against the under surface of the ice. However, since there was a small space between the top of the target and the Weston cells, and since ice normally rests in, rather than above, the water, it is apparent that the actual water-ice interface was above the cells. Therefore any loss which this interface, per se, may have caused would have been calculated as part of the loss in transmission through the ice. It seems probable that such loss was small.

Furthermore, the existence and amount of any extra loss in the uppermost thin layer of water, under the ice, is difficult to estimate. The difficulty of accurately gaging the depth of the target (within the

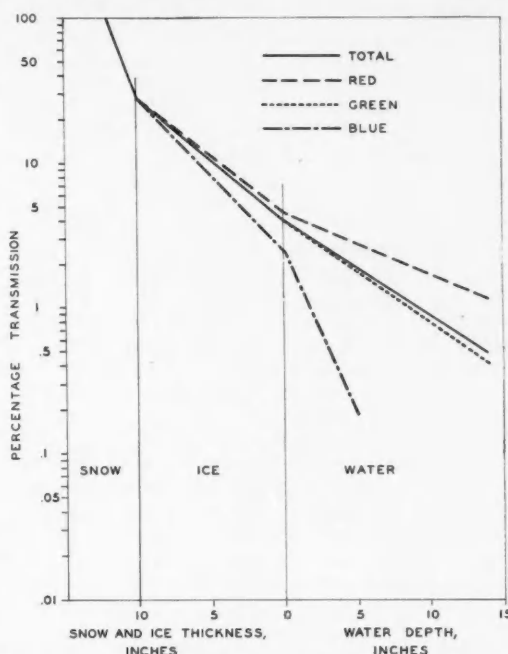


FIG. 30. Percentage transmission of light of different wave lengths through snow, ice, and water. Bog Lake, March 13, 1941.

first one or two feet below the ice), combined with the possibility of error caused by stray light from the side, prevented the precision of measurement necessary to determine the exact behavior of the water immediately under the ice. Another possibility about which only speculative statements can be made is that of reflection of light back into the upper water from the under surface of the ice (or of the snow).

In general, on the basis of the data as they appear in Table 6 and in Figures 28 and 29, it was apparent that there was no very great difference in the percentage absorption of a given thickness of water in the upper layers as compared with the same thickness in the deeper layers. The slight tendency toward such a difference in Bog Lake possibly can be accounted for by the greater amount of suspended material in the upper water.

TRANSMISSION THROUGH ICE

Of much greater and more striking effect in absorbing light is the cover of ice and snow. The measurements made of light transmission through snow and ice are given in Tables 6-9. Table 7 is a summary of the percentage transmission through ice of various thicknesses and conditions, arranged in descending order of percentage. The values ranged from 84 percent, for 7½ inches of very clear ice, to 2.0 percent for 15 inches of partly cloudy ice.

The figures in this table compare fairly well with the few data which are to be found in the literature. Sauberer (1938) found the transmission through 25

mm. (1 inch) of clear ice to be about 84 to 87 percent, and through 4 cm. ($1\frac{1}{2}$ inches) of "sehneis" to be about 45 percent. The figures given by Croxton, Thurman, & Shiffer (1937) are: 4 inches, 86 percent; 6 inches, 66 percent; and 14 inches, 33 percent. Zinn & Ifft (1941) gave the result of only one measurement; through $4\frac{1}{2}$ inches of ice, with a "slush cover," approximately 65 percent of the incident light penetrated. Chandler (1942) found 58 percent transmission through 40 cm. (16 inches) of ice, a percentage transmission equivalent to that through the same depth of Lake Erie water with a turbidity of about 20 p.p.m. The data of these various writers were obtained by the use of instruments and techniques which varied somewhat with each other, but in general they probably are properly comparable.

It is readily apparent (from Table 7) that the penetration of light through ice varies greatly with the condition of the ice. For example, $7\frac{1}{2}$ inches of clear ice transmitted 84 percent, as against 22 percent for $7\frac{1}{2}$ inches of "partly cloudy" ice. Only 7.2 percent of the incident light passed through $10\frac{3}{4}$ inches of ice described as "very cloudy." This ice was full of minute air bubbles, which gave it somewhat the appearance of opal glass, and rendered it probably as opaque as any ice likely to be encountered on natural waters, except that which might have inclusions of dirt or other foreign matter. Similarly, the "clear" ice just mentioned was probably as crystal-clear as any which ever freezes on inland lakes. Between these two extremes, the ice of most lakes varies greatly in character, and in ability to transmit light, depending on the manner in which it was frozen, on various thaws and refreezings, and so forth. The approximate range of percentage transmission through various types of ice is delimited by Table 7.

As with water, it is probable that a part of the total loss of light in passing through ice consists of "surface loss." For ice this loss is largely undefined and unmeasured. If the usually rather dark appearance of the ice on a lake (especially if the ice is clear) may be used as a criterion, surface reflection apparently is of relatively small amount, and it is probable that most of the total loss actually occurs within the ice. At any rate, and of necessity, the data given here in regard to light absorption by the ice include whatever loss may take place both at the upper surface of the ice and at the water-ice interface.

It is assumed that the transmission of light through ice, if the ice is uniform in character throughout, probably takes place according to a mathematical relationship such as that described above for water. Following this assumption, the points on the graphs of Figures 28-30, representing the percentage amount of light entering the ice and that emerging from it, respectively, are connected with a straight line, the slope of that line indicating the relative light-absorbing power of the ice. Comparative lines of this sort

have been drawn, in Figure 28, for several of the lakes studied.

The transmission of light through ice apparently varies somewhat with the region of the spectrum. As stated by Dorsey (1940, p. 398), ice in large masses has a blue appearance, probably caused by light scattering. Sauberer (1938) found very little difference between the various spectral bands, in transmission both through clear ice and through "sehneis." In the data of Table 7, the clearer ice showed no significant differences in relative transmission of light of different colors. However, the more turbid ice showed a pronouncedly lower relative penetration of blue light. Apparently, therefore, a proportionately large loss of blue light is associated not so much with pure ice as with included particles, such as air bubbles, or possibly (in the case of the ice of Bog Lake) particles of coloring matter which may have become frozen into the ice. In Figures 29 and 30, the slightly different slopes of the lines for the transmission of various colors through the ice of East Lake and Bog Lake are evident.

TRANSMISSION THROUGH SNOW

The penetration of light through snow is considerably harder to measure accurately than that through ice or water, not only because of the difficulties of making observations under natural conditions (i.e., without disturbing the snow), but also because of the exceedingly many variations in the character of the snow. However, the information obtained is of value in establishing a general range for snow, and thus in showing the relative absorption by snow, ice, and water.

With the exception of one series of experimental determinations, the measurements of light transmission through snow made during the course of this study were performed on the ice of various lakes, without disturbing the natural snow cover. Thus they are of necessity indirect measurements; that is, the value was calculated from the transmission through snow plus ice, compared to that through the ice alone, after the snow had been removed. Probably the only significant error, however, is that caused by surface loss from the ice (see above), and this loss likely is small.

Kalitin (1931) made an extensive series of measurements by placing the target of a photometer on an open field, and allowing the natural snowfall to cover it. The chief difficulties in interpreting the data so obtained lie in the variations in amount and quality of light from time to time, and the changes in the character of the snow between readings. Most of the remainder of the few observations which have entered the literature have involved some sort of an artificial set-up, with consequent disturbance of the snow. However, in spite of variations in procedure and apparatus, the measurements made by the various writers may be used to form a general idea of the light-transmitting qualities of snow.

The reflection of light from the surface of snow is

very much greater than that from water or ice. The albedo, expressed as the ratio of reflected light to total incident light, varies, according to the tabulation by Dorsey (1940, pp. 486-487), from 40 or 50 percent to over 90 percent. Thams (1938) gave for new snow 82 percent, for old snow 60 percent, and for melting snow 50 percent. Sauberer (1938) found new snow to have an albedo of about 84 percent, and old snow about 72 to 76 percent. The figures of Kalitin (1930, 1931) range from 52 percent for old, grainy snow, to 87 percent for fresh, dazzling white snow. Considerable and rapid changes were noted by this author. After experimental wetting of the snow surface, the albedo was 52 percent. Hand & Lundquist (1942) gave values up to 89 percent for clean white snow.

In the measurements of this investigation (Tables 6, 8, and 9), separate account was not taken of the loss from the snow surface; the figure given in each instance is that for the amount of light which emerged from the bottom of the snow layer, expressed as a percentage of that incident upon the upper surface. Stated as true percentage transmission through the snow, the ratio would be larger. However, since the concern of this study is with the amount of light ultimately passing through the sequent snow, ice, and water, the amount of loss by reflection at the surface of the snow is of interest chiefly in helping to explain the tremendous power of snow to reduce light intensity.

In Table 8 are summarized the snow transmission measurements on the various lakes. Percentage transmission varied from 28 percent for 1 inch of slushy snow, to 0.7 percent for 10 inches of dry snow. Crusted snow apparently allowed somewhat less penetration than light, dry snow.

Table 9 shows the percentage transmission through snow artificially placed on the photometer target. A thickness of 1 inch permitted only about 4 or 5 percent of the light to pass through it; at 4 inches only a slight trace of light remained. These figures are subject to the possible error caused by the use of light of relatively low intensity (incandescent bulb); the transmission percentages thus may be proportionately somewhat low (see reference, below, to Croxton et al.).

Figures from the literature are somewhat scattered. Thams (1938) recorded 13 percent transmission for 10 cm. (4 inches) of snow, and 0.6 percent for 50 cm. (20 inches). These figures are somewhat high as compared to those of other workers. The transmission found by Croxton, Thurman, & Shiffer (1937), using snow artificially placed above the photometer, varied from 11.7 percent for 1 inch, to 0.03 percent for 7 inches. These latter writers found a lower percentage transmission for light of low intensity, and considerable differences caused by differences in the quality of the snow. Clean and fresh snow allowed the greatest penetration, clean but wet snow the next greatest, and granular snow the least. This order agrees with the findings of Hand & Lundquist

(1942), that within a certain range the higher the water content of the snow the less light transmitted. The figures given by Hand & Lundquist, for "fine granular compact" snow, range from 22.3 percent for $\frac{1}{2}$ inch, to 1.2 percent for $5\frac{3}{4}$ inches. Kalitin (1931), in a table of summary, gave percentage transmissions ranging from 21.7 percent for 2.5 cm. (1 inch), to 0.09 to 0.03 percent for 62 cm. (about 24 inches). Again wet snow was found to transmit light less freely than did dry snow.

It is not certain in all cases, but apparently all of the figures given above were based upon total amount of incident light (rather than upon that remaining after surface reflection loss), as also are the figures of the present study. That means, then, that wet snow transmits less of the total incident light than dry snow, in spite of the fact that dry snow has a higher loss by surface reflection.

Figure 31 shows the relative light-transmitting properties of snows as measured by various observers. The assumption is made that a logarithmic relationship holds between depth of snow and percentage penetration. This assumption has been made by Sauberer (1938), who gave an actual absorption coefficient. If the assumption is true, then the relative slope of the lines on Figure 31 give an indication of the relative powers of these various snows to absorb light.

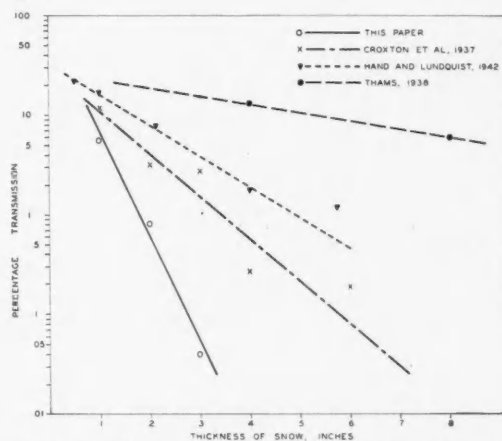


FIG. 31. Percentage transmission of light through snow. Data from authors.

Each of these lines, produced to the axis of the graph, would intercept the axis below the 100 percent mark. The difference, presumably, represents that part of the light which was lost in surface reflection.

Figure 28 is a composite diagram of the combined effects of snow, ice, and water in diminishing light intensity. Starting at 100 percent of incident illumination, each line shows, first, the drop in intensity caused by the snow, next the further drop in passing through the ice, and finally the diminution caused by the water. The plotted value for percentage inten-

sity at any point on the line represents, theoretically, the amount of light penetrating to that particular depth of snow, ice, or water. The line for Crater Lake (based on data from Utterback, Phifer, & Robinson 1942, and Brode 1938) does not include ice, since the water was open at the time of observation.

The tremendous differences in the amount of light reaching various depths under different conditions of snow and ice are apparent from the figure. For example, for the dates given for the respective lakes, Clear Lake received more light at the 32-foot depth (1.1 percent transmission) than did Bog Lake at 1 foot under the ice, and 22 times as much as South Londo Lake just under the ice (0.05 percent). The light penetrating to the bottom of East Fish Lake (under the given set of conditions) was only 0.03 percent of that which reached the top of the snow cover. That percentage transmission was only about one-fourth as much as that to a depth of 120 meters (about 400 feet) in Crater Lake (data from Utterback et al. 1942).

In terms of foot-candles of light falling upon the target of the photometer (see under Methods), a few sample readings, taken from Table 6, are: of 7,600 foot-candles falling upon the snow on South Londo Lake (March 5, 1941), only 4 f.c. penetrated the ice plus snow. At Clear Lake (February 23, 1941) an incident illumination of 8,000 f.c. resulted in the penetration through the ice of 6,700 f.c., or 84 percent, and to the bottom of the lake (30 feet) of 112 f.c., or 1.4 percent. Thus 1,700 times as much light penetrated $7\frac{1}{2}$ inches of clear ice with no snow (Clear Lake) as was transmitted through 24 inches of partly cloudy ice covered with 10 inches of snow (South Londo Lake).

The transmission of light through snow apparently varies somewhat with the region of the spectrum. Sauberer (1938) found the relative penetration to be the greatest in the green-yellow portion of the spectrum, and to fall off in the blue and slightly in the red. Kalitin (1931) stated that absorption of light by wet snow is greatest in the longer waves (the red). The somewhat scanty data of the present study (Tables 8 and 9) apparently show a somewhat reduced penetration in the red and blue spectra.

RELATION TO PHOTOSYNTHESIS AND DISSOLVED OXYGEN

In spite of considerable work by various investigators, comparatively little exact information is available regarding the quantitative light requirements of aquatic plants under various conditions. It is extremely difficult, in measuring these requirements, to control all of the necessary factors. It is evident, however, that for any given set of conditions there must exist an intensity of light which will promote photosynthesis, and below which photosynthesis will be overbalanced by respiration. Such an amount of light has been termed the compensation intensity.

Clarke (1939) cited references which placed the compensation intensity (plant species and other factors not stated) at about 350 to 500 lux (approx-

mately 30 to 45 foot-candles). Wilson (1935) found the lower limit of certain types of aquatic vegetation, in a lake in Wisconsin, to be at a depth at which the light amounted to from 4.4 to 6.8 percent of the "total sunlight at zenith"—that is, at roughly 400 to 600 foot-candles. It seems likely, however, that factors other than light intensity also operated to limit the maximum depth of growth of these plants. Pearsall & Ulyott (1934) found rooted vegetation to be adversely affected when the light intensity was cut down from about 4 or 5 percent to about $1\frac{1}{2}$ or $2\frac{1}{2}$ percent.

Little is known about the light requirements of the phytoplankters of inland lake waters. Probably there are considerable differences among the various species, and such factors as temperature must have a certain effect. However, some of the figures given in Table 6 for the amount of penetration of light through snow plus ice cover are such small fractions of the amounts proposed as general aquatic plant compensation intensities, that it seems almost certain that such small amounts of light could not maintain a favorable balance of photosynthesis over respiration and decay. On the other hand, there appears to be reason to suppose that the amount of light which penetrates even $1\frac{1}{2}$ to 2 feet of moderately clear ice (with no snow cover) is enough to satisfy the requirement for photosynthesis.

Photosynthesis is controlled to a large degree by the quality, as well as the quantity, of light. In general, red light is more effective than that of shorter wave lengths. Some aquatic plants, however, such as certain diatoms, have been found to be able to utilize almost any part of the visible spectrum (Jenkin 1937). As discussed above, there are certain differences in the transmission of light of various wave lengths through ice and snow. However, in general these differences are relatively small, and it is probable that the more important effect of the ice and snow is that of reducing the total quantity, rather than of changing the quality, of light.

The measurements of light penetration made during this study were too limited in number to justify any attempt to show a correlation between light intensity and oxygen production which would be expressible as a mathematical function. However, as is discussed above, a definite connection is demonstrable between the dissolved oxygen in the water and the amount of snow on the ice; and in this manner the effect or the oxygen tension of the water of changes in the light intensity on the oxygen tension of the water is clearly shown. It appears conclusively evident that a heavy snow cover upon the ice so greatly reduces the amount of light entering the water that photosynthesis by the phytoplankton virtually ceases, with a consequent and almost certain reduction in oxygen production.

EXPERIMENTAL STUDIES

PUMPING EXPERIMENTS, PREVIOUS WORKERS

Experimental aeration of water under the ice has been attempted by various workers. In Iowa, in 1935

and 1936, air blowers were used (Aitken 1938). These blowers delivered a large volume of air, under fairly low pressure, into the water. They were not very successful, however. Presumably a relatively small part of the air actually went into solution in the water. In the same state in 1936-37, pumping water into the air was tried, the object being for this water to absorb or entrap air and carry it back into the lake. The method was held to be impractical for aerating large lakes.

Various pumping procedures have been tried in Minnesota and Wisconsin. Some small success attended the experiments in which a stream of water and one of compressed air were mixed at the point of entrance into the water. However, here again it was found that the method was not suitable for aerating large bodies of water.

In Michigan, during the severe conditions of the winter of 1935-36, the Institute for Fisheries Research attempted experimental aeration by means of a stream of water pumped from the lake, sprayed into the air, and allowed to return through holes cut in the ice. This experiment has been referred to by Hubbs & Eschmeyer (1938). Although the water at the point of entrance through the ice was found to have a very much increased oxygen content, this increase was transitory, and disappeared within 28 hours. Furthermore, the effect was very local, indicating the method to be of small value for application to any considerable area.

PUMPING EXPERIMENT, PASINSKI'S POND

Pasinski's Pond was used, in February and March, 1940, for an experiment in aeration by means of a pumped stream of well water. The pond is described above; Figure 6 is a map showing its outline, depth contours, and the location of sampling stations. Although the pond is one simple basin, it has been found convenient to divide it, for the purpose of interpreting certain data, into two parts, the north end (containing the pump) and the south end (including the outlet). This division is based upon the vegetation present. The south end contains large beds of filamentous algae (principally *Spirogyra*), as well as an almost solid mat of *Anacharis*. Algae are practically absent from the north end, which has, however, a fair amount of *Anacharis*. These weed beds of course are more distinctly to be observed during the summer months.

At the start of the winter of 1939-40, only one sampling station was used (Station 15, in the north end). This station was about 75 feet from the point of discharge of the pump. The dissolved oxygen at this station (the surface sample) dropped rapidly and steadily, from 19.1 p.p.m. on January 7, to 0.5 p.p.m. on February 10 (see Figure 32).

On February 10 the pump was set into operation, pumping about 60 gallons per minute. The well water as it came from the pump carried only about 1.5 to 2.0 p.p.m. of dissolved oxygen, but by running through wire mesh and over an inclined trough it increased its oxygen content to about 4 to 6 p.p.m.

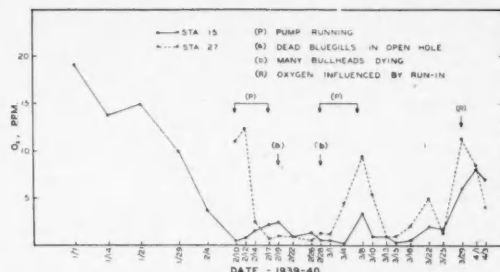


Fig. 32. Dissolved oxygen, effect of pumping water. Pasinski's Pond, Station 15 (north end) and Station 27 (south end). Surface samples, 1939-40. See text.

Its temperature was approximately 50° F. (10° C.).

The pump was operated continuously for seven days, until February 17. During that time the discharge from the pump melted a hole through the ice at the edge of the pond, roughly 8 or 10 feet in diameter. This hole remained open during the time that the pump was running, and for two or three days afterward; it constituted the "open hole" to which reference is made elsewhere in this paper.

On February 10, about 25 stations were established, in a sort of geometric design, in the north end of the pond, and three stations in the south end. A few more stations subsequently were added. Samples were taken at these stations, at intervals of from two to four days, from February 10 until April 1. Uniformly, the samples were surface samples, except that enough check samples were taken from other depths to show that the highest oxygen values always were to be found in the upper water (see discussion, below, on dissolved oxygen consumption in lakes).

After having run for seven days, the pump was turned off on February 17. It was started again on February 28, and ran continuously until March 6.

The original idea was to use the south end of the pond as a control, to determine the amount of aeration accomplished in the north end by the pump. This plan was found to be faulty, however, since initial conditions in the two ends of the pond were different. Presumably because of the activities of the algae in the south end, the water there had much more dissolved oxygen at the start of the experiment than did that at the north end.

The dissolved oxygen data of the experiment are not amenable to most methods of statistical treatment. Average values are scarcely valid, since there was much fluctuation between stations, and also since too few stations in the south end were used. However, Figure 32 is of some help in interpreting the possible effect of the pump. On this figure are shown the dissolved oxygen values for Station 15 (north end) and Station 27 (south end). In accordance with the above explanation, these two stations do not necessarily represent the average values of the two ends of the pond, but they may be considered somewhat typical.

At the time the pump was first put into operation, on February 10, the oxygen was much higher at Station 27 than at Station 15, but was declining rapidly at Station 27. Either under the influence of the pumping or for some other reason, the oxygen gradually increased at Station 15 until February 19, when it was 2.4 p.p.m.; meanwhile that at Station 27 had gone down to a low of 0.7 p.p.m. on February 17. From February 22 until March 1 the oxygen remained quite low at nearly all stations in the pond, in spite of the fact that the pump was again put into operation on February 28.

From March 1 until March 4 there was a rise in the oxygen at Station 27, as well as at other stations in the south end; while the oxygen at Station 15 and at most other stations in the north end still remained low, in spite of the pumping. Then, from March 4 until March 8, there was a sharp increase in oxygen at both ends of the pond. As shown by the curves of Figure 32, this increase was larger and began earlier in the south end. It probably was due to renewed photosynthetic activity, since nearly all of the snow by this time had left the ice. The south end of the pond, containing more algae, responded much sooner and to a greater extent to changes in light intensity than did the north end.

The peak values on March 29 presumably were occasioned in part by inflowing water from rain and melting snow.

There is further evidence that the pumping had very little if any beneficial effect. On the sampling dates during the first period of operation of the pump, February 10 to 17, only seven samples of all those taken in the north end (Stations 1 to 23) had 2.0 p.p.m. or more of dissolved oxygen. None had over 2.8, and most of them ranged from 0.2 to 1.5 p.p.m. Of the samples from the ten stations nearest the pump, only two had 2.0 p.p.m. or more, and oxygen values as low as 0.3 p.p.m. were found within 20 feet of the discharge point of the pump after four days of operation.

Pumping 60 gallons per minute, or about 11,000 cubic feet per day, the pump would displace approximately one-fortieth of the volume of the pond per day (assuming that the pumped water did not set up a current which would shunt it to the outlet). If the pumped water, containing about 5 p.p.m. of dissolved oxygen, became completely mixed with the pond water, it could (theoretically) raise the oxygen content of the entire volume of water approximately one-fortieth of 5.0 p.p.m., or about 0.125 p.p.m., per day,⁴ or about 0.9 p.p.m. on 7 days. Or if it is arbitrarily assumed that only (say) the northern one-third of the volume of the pond were affected, then the oxygen content at that end could be raised about 2.7 p.p.m. in 7 days.

It is quite evident that no such increase took place during the period February 10 to February 17. Pre-

⁴ Obviously the pumped water, carrying only 5.0 p.p.m. of oxygen, could increase the oxygen in the pond water only if the latter had less than 5.0 p.p.m. to begin with; and the full amount of the increase given in the computations above could come about only if the pond water had zero oxygen at the start.

sumably the explanation lies in the high oxygen demand which had been built up in the water. Very little oxygen, if any, was being produced by photosynthesis in the north end of the pond, and an oxygen demand existed which could not be overcome by the efforts of the pump.

If the pump were operated for long periods of time (a somewhat expensive and troublesome procedure) it probably would be of considerable help in forestalling the development of serious conditions. But once those conditions have developed in the pond, pumping well water apparently is almost useless.

On February 14, four days after the pump first was started, there were several bluegills in the open hole, alive but not very active. On February 19, two days after the pump was turned off, the open hole contained hundreds of dead bluegills. Mortality struck suddenly, for on February 17 there were few if any dead fish. Apparently all or most of the bluegill population died within a few days, for no dying or newly dead bluegills were observed during March.

The bullheads began to die somewhat later than did the bluegills. Very few dead bullheads were seen in early February, but on February 28 many were dead or dying. The mortality of the bluegills apparently was complete, for intensive seining the following summer failed to take any. Only a part of the bullheads died. Altogether some 13,000 bluegills and over 1,000 bullheads were killed.

SNOW REMOVAL, HATCHERY PONDS

Three of the small experimental ponds at the Drayton Plains hatchery were used for the experiment here described. Early in December, 1939, these ponds were filled with water from the river, to a depth of about 2½ feet. In order to maintain the water level, a small flow was permitted to run into and out of each pond. This flow remained somewhat larger than was intended, and affected the results of the experiment to a certain extent. However, the flow was about the same in each pond.

The three ponds were allowed to remain undisturbed, except for the taking of samples, until February 12. On that date the snow (about 3 inches in depth) was shovelled cleanly off the ice of Pond 10. From that time on, the snow was removed from this pond soon after each new snowfall.

On February 17 the ice on Pond 8 was completely covered with a layer of opaque building paper, which was held in place with snow. The paper stayed in place very well until the breakup of the ice.

Pond 9 was left unmodified throughout the experiment, as a control.

From January 7 until the breakup of the ice, dissolved oxygen samples were taken periodically in all three ponds. The sampling depth was 1 foot. In Figure 33 are shown the dissolved oxygen curves.

In view of the fact that the three curves stayed so closely together until the beginning of experimental conditions, their divergence after that time seems to be definitely significant. Evidently the amount of light entering the water did have an appreciable effect

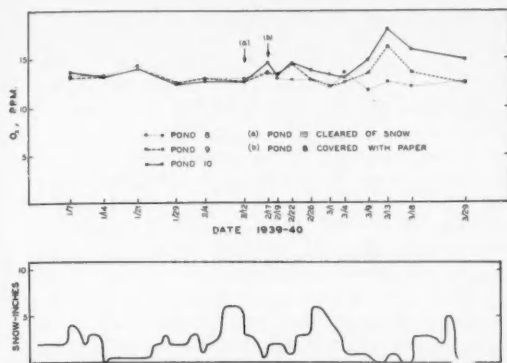


FIG. 33. Dissolved oxygen and snow cover. Snow-clearing experiment, hatchery ponds, 1939-40. See text.

upon the dissolved oxygen. It is only reasonable to suppose, furthermore, that this effect would have been much greater had there not been a continuous partial displacement of the water.

It seems probable that the differences between the curves for the three ponds were not due so much to diminution of oxygen in Pond 8 (probably the inflowing water carried enough oxygen to satisfy the relatively small oxygen demand present), as to the greater oxygen production in Ponds 9 and 10. The amount of light entering Pond 9, through the snow-covered ice, apparently was enough for some photosynthesis (it must be remembered that for a time in early March the ice of Pond 9 was bare or nearly so), and the water in Pond 10, with the snow removed, received more light and did still better in oxygen production.

SNOW REMOVAL, GREEN LAKE

On January 22, 1943, the snow on a roughly measured one-acre area of Green Lake was melted down by means of a stream of water pumped from beneath the ice. For this work a centrifugal pump was used, with a capacity of about 3,000 gallons per minute, and driven by an air-cooled gasoline motor. The intake pipe of the pump was thrust through a hole in the ice, and the outflow took place through a 2½-inch rubber-lined canvas hose about 20 feet long. In order to cover the area, which was rectangular, roughly 300 feet by 150 feet, the pump had to be moved from one position to another about 8 or 10 times. Laying off the plot, chopping holes for the pump, and performing the actual pumping took two men about 7 to 8 hours.

Part of the time the water was sprayed onto the surface of the snow in a very coarse spray, and part of the time it simply was allowed to run from the open end of the hose out onto the ice, through and under the snow. The former method was only slightly more effective, and involved more effort than the latter.

At the time of the pumping, the snow over most of the lake was from 8 to 10 inches deep, including the

slush, which came in most places to within 3 or 4 inches of the surface of the snow.

No effort was made to completely melt the snow to water. Rather, it was only wet down into a thin slush. The difference in appearance between the treated and untreated areas is shown in Figure 34. The slush formed by the pumping subsequently froze into firm, although rough and somewhat cloudy, ice. As has been mentioned above, even cloudy ice has many times the light-transmitting ability that snow has.

It was intended, of course, that the untreated area would serve as a control, and that parallel oxygen determinations in the days following the experiment would show the effect, if any, that the melting of the snow had on the dissolved oxygen. However, in the two days from January 22 to 24 the snow over most of the lake virtually disappeared, through natural causes. A few small local areas retained from ½ to 2 inches of snow for a few days, and some of these



FIG. 34. Contrast between flooded and nonflooded areas in the snow. Green Lake, January 22, 1943.

were utilized for oxygen determinations, but to all practical intent the desired control was lacking.

Dissolved oxygen figures (averages) for several stations within and outside of the treated area, on three sampling dates following the experiment, are given in Table 10. These data show an apparent slight trend for the oxygen to be higher in the treated area than outside of it. Because of the circumstance just described, however, no significance can be attached to this seeming difference. Furthermore, even within the treated area the oxygen declined somewhat in the ten days after the pumping. Thus if the light which penetrated the ice actually was sufficient to produce oxygen, it was not capable of quickly overcoming the serious oxygen-depleting conditions which had arisen.

TABLE 10. Snow removal experiment, Green Lake, 1943. Dissolved oxygen, p.p.m., average values for stations within and outside of treated area. Number of stations averaged and range of values, in parentheses.

Date	SURFACE SAMPLE		2-FOOT SAMPLE	
	Inside	Outside	Inside	Outside
1/22*.....	(4) 5.2 (4.2-6.4)	(1) 6.1	(1) 2.5	(1) 2.5
1/24.....	(10) 6.4 (4.3-11.2)	(7) 4.6 (3.2-7.2)	(7) 3.1 (1.8-4.9)	(7) 1.7 (0.6-2.3)
1/29.....	(10) 3.8 (3.0-4.7)	(7) 2.9 (2.0-3.8)	(7) 2.5 (2.1-2.8)	(7) 1.9 (1.1-3.1)
2/2.....	(5) 3.2 (2.8-3.7)	(5) 2.3 (1.1-3.7)	(3) 2.1 (1.8-2.3)	(5) 2.0 (1.0-3.0)

*Before pumping, January 22.

By about February 5 the lake as a whole apparently had reached its low point (as regards dissolved oxygen), and recovery from that time on was general and fairly rapid. There was no appreciable amount of snow on the ice most of the remainder of the winter.

THE OXYGEN BALANCE OF AN ICE-COVERED LAKE

The relative abundance or lack of dissolved oxygen is so definitely a controlling factor in the life processes in an ice-bound lake that careful consideration should be given to the various agents which act to lower or raise the dissolved oxygen content. The following discussion attempts to collate some of the information to be found in the literature, as well as certain observations of the present study.

Two diametrically opposed sets of processes exist and usually are concurrently active—those which consume oxygen, and those which replenish it. The precarious balance between the two is fine indeed, and when this balance is upset the consequences may be sudden and intense. The action of these processes is greatly influenced by the low temperature of the water in winter. Also it is limited considerably by the ice cover, and by the almost complete immobility which arises from thermal stratification and lack of wind agitation. Except for these modifications, the processes of oxygen utilization and oxygen renewal

are in general the same processes which exist in the summer.

OXYGEN CONSUMPTION

RESPIRATION OF FISH

It is a rather common concept that the respiration of the fish is a chief factor in the diminution of the dissolved oxygen. In occasional instances this may be true. Some bodies of water, such as pot-holes, rearing ponds, and so forth, may have an extremely high concentration of fish. Koehs (1891) estimated the fish in certain wintering ponds to amount to 1 to 1½ kilograms per cubic meter of water, which is roughly equivalent to 2,700 to 4,000 pounds per acre-foot. Certainly such an amount of fish would consume an appreciable quantity of oxygen, even at winter temperatures. However, such quantities are rather exceptional. The concentrations of fish in lakes such as those of the present study are on the order of a few hundredths of the extreme figure given above. Even in organically rich, shallow ponds of this region, probably a standing crop of 75 to 100 pounds per acre-foot is very rarely exceeded.

There is scant information available concerning the oxygen requirements of fish at near-freezing temperatures. Some of the data of the literature are summarized in Table 11. Probably the average value for the warm water fishes commonly found in southern Michigan waters (such as black bass, sunfish, suckers, yellow perch, etc.), for the temperature range 0°-4° C., is somewhere between the highest and lowest of the figures given in this table.

TABLE 11. Oxygen requirements of various fishes at low temperatures.

Fish	Temp., °C.	O ₂ consumed, cc./kg./hr.	Author
Brown trout.....	4-7°	102.5	Gardner & Leetham (1914)
Goldfish.....	2°	14.8	Regnard (1891)
Goldfish.....	5-6°	16.07	Gardner & King (1923)
Tench.....	0°	6.05	Linstedt (1914)
Pike (<i>Esox lucius</i>).....	5-6°	24.44	Gardner & King (1923)
Eel.....	5-6°	9.28	Gardner & King (1923)

For purposes of comparison, it is perhaps of interest to make a rough theoretical computation of the amount of oxygen used by the fish in a given body of water. During the winter of 1939-40 Pasinski's Pond had an average volume, excluding ice cover, of approximately 350,000 cubic feet (9,900 cubic meters), or about 8.0 acre-feet. This amount of water weighs 22,000,000 pounds. If it were saturated with dissolved oxygen, at 0° to 4° C. (i.e., with about 14 p.p.m.), the water in the pond would contain about 300 pounds of dissolved oxygen. Suppose there were in the pond 500 pounds of fish (62.5 pounds per acre-foot). This is a hypothetical figure, and probably is too high. Using the also hypothetical figure of, say, 25 cc./kg./hr. (equal 0.000036 lb./lb./hr.) for the average oxygen consumption of the bluegills and bullheads in the pond, the figure obtained for the oxygen used by the fish is 0.018 pounds of oxygen per hour, or 0.43

pounds per day. At that rate, 300 pounds of dissolved oxygen would meet the respiratory needs of the fish for 700 days (actually, of course, the fish would be unable to utilize the last of the oxygen, because of their inability to extract it at low tensions).

In comparison, Koehs (cited above), using the value given by Regnard of 14.8 cc. of O₂ per kg. of goldfish per hour, and the (slightly too low) figure of 10.58 p.p.m. for dissolved oxygen at saturation, obtained the theoretical result that the water in the carp wintering ponds which he was studying held only a 20-day supply of oxygen for the fish.

It seems rather certain that in the average Michigan lake of the winter-kill type the fish play a very minor part in the depletion of the dissolved oxygen under the ice. The respiration of other aquatic vertebrate animals also has little influence upon the oxygen supply, since most of them, with the exception of tadpoles and immature salamanders, are air-breathing.

RESPIRATION OF INVERTEBRATES

It is extremely difficult to evaluate properly the part played in the oxygen depletion of a lake by the respiration of invertebrate animals, since the two chief governing factors, the number of organisms present and the oxygen requirements of each, are to a large extent unknown. Especially is this true in the winter.

Comparatively few quantitative studies of winter zooplankton have been made. There is considerable variation from lake to lake and from one winter to another. In general, however, the total zooplankton is usually at a minimum in winter. Very few of the larger zooplankters (copepods, daphnids) have been found to display winter pulses, and these probably are transitory or local. Naber (1933) concluded that the plankton animals perform a very small part of the removal of oxygen from a lake. Considering the small size of these animals, and the reduction in their oxygen requirements brought about by low temperatures, it is likely that their respiration accounts for an insignificant portion of the oxygen consumed during the period of ice cover.

The bottom-dwelling invertebrates usually are more abundant in winter than in summer, since many insects pass the winter as aquatic larvae or nymphs. These immature insects may be present locally in almost prodigious numbers, an example being the concentrations in places in many Michigan lakes, of burrowing mayfly nymphs. Midge-fly larvae often are present in many hundreds or even thousands per square foot of bottom. Since winter is a time of growth and activity for the aquatic insects, they require a certain amount of oxygen, even at low temperatures.⁵

With the exception of an occasional concentration, most other benthic invertebrates are present in much smaller numbers. Relatively large forms, such as

crayfish, mussels, or the like, probably are rather lethargic in winter.

No matter what the total oxygen-consuming power of the bottom animals, it is obvious that they can have a direct oxygen-depleting effect upon only the thin layer of water in direct contact with the bottom (the indirect transmission of this effect, as set forth in the microstratification theory, is discussed below). Of the sporadic migrations of bottom dwellers into the upper water, little mention need be made. When occasioned by adverse conditions near the bottom, as they often are, these migrations may be said to represent mainly an effect, rather than a cause, of oxygen diminution.

On the whole it seems probable that, compared to the amount of oxygen used by the decay of dead organic material, that consumed by the respiration of invertebrates is a proportionately small amount.

RESPIRATION OF PLANTS

Living plants, both macrophytes and plankton algae, use oxygen for respiration. Under the proper conditions, these plants produce much more oxygen than they use. When adverse conditions arise, however, oxygen production falls off, and eventually is over-balanced by oxygen consumption. It is difficult to say at what point a plant can no longer be considered to be in a living state, and beyond which its oxygen-consuming process is one of decay rather than of respiration. However, for purposes of present discussion, it is perhaps justifiable to represent most of the oxygen demand of the plants under the ice as being occasioned by their decomposition, whether or not they are in a strict sense dead.

Not usually thought of in the flora of a lake are the actinomyces of the genus *Micromonospora*, which have been shown by Umbreit & McCoy (1941) to be rather numerous in several Wisconsin lakes, and which are believed by these authors to play a definite part, although probably a small one, in the dissolved oxygen cycle. Their importance probably lies in the quality, rather than in the quantity, of organic material which they oxidize, since they have the ability to attack such usually resistant materials as chitin, lignin, cellulose, and so forth.

Fungi also often are present in lake water, but it is doubtful that they ever reach sufficient concentrations to be very important as an agent in oxygen depletion. The activities of the water and bottom mud bacteria are discussed in the sections below.

DECAY OF BOTTOM MATERIALS

The role of decomposition of bottom materials in the utilization of oxygen is a very important one, and has been the subject of much discussion. The relative importance of the organic matter in the lake bottom and that suspended or dissolved in the water is somewhat speculative, and various divergent views have been expressed.

It has long been known that in winter, as well as in summer, the water near the bottom of a lake is more apt to be lacking in oxygen than that nearer

⁵ It must be remembered that the temperature on or near the bottom usually is 3°-4° C. higher than that just under the ice, probably a significant amount as related to metabolism. For that matter, inhabitants of the profundal regions of deeper lakes live, the year around, at temperatures only slightly above 4° C.

the surface, and many writers have associated this difference with the decomposition of the bottom mud. In this connection it is of interest to note that, as discussed above, the lines of equal oxygen concentration tend to follow the bottom contour of the lake in their configuration.

Drown (1892) found, in the oxygen content of the water in several ponds in the winter, variations which appeared to have a connection with differences in the composition of the bottom materials, and concluded (p. 341) that "it is the character of the bottom of the pond, rather than the organic matter in solution and suspension in the water, which determines the amount of oxygen remaining in solution." Birge & Juday (1911) observed that the greatest decrease in oxygen, in winter, was near the bottom, and indicated that bottom decay is an important factor. Miyadi (1934) said (p. 236): "It is a recent common opinion to esteem the bottom deposit higher than the decaying plankton organisms sinking down from the epilimnion in diminishing the oxygen of the deep water." And Henrici (1939) made the well-nigh dogmatic statement: "It is the tremendous oxygen-consuming power of the large numbers of bacteria in the lake bottom which . . . causes oxygen to disappear below the thermocline in stratified eutrophic lakes, which causes fish to suffocate in shallow lakes in the winter."

In his microstratification theory Alsterberg (1927) gave the decay of bottom materials as the chief cause of oxygen depletion in the deeper water of a lake, particularly in the thin layer of water lying directly on the bottom. The oxygen lack of this microstratum is gradually transmitted, he believed, into a deficiency in subsequently shallower layers through water movements brought about by wind or otherwise. As Welch (1935, p. 121) has pointed out, this transmission might be produced in an ice-covered lake by the rising of gas bubbles from the bottom or by convection currents. These convection currents under the ice have been held by Mortimer (1941-1942) to produce "turbulent eddies," which tend to diffuse dissolved substances and to transmit to upper layers of water the oxygen reduction which occurs at the water-mud interface.

In regard to the vast potentialities on many lake bottoms for the consumption of oxygen, there can be no question. In the deeper portions of most eutrophic lakes, and indeed throughout the entire area of many shallow lakes, the bottom is heavily blanketed with a soft, semi-organic material variously termed "muck," "peat," "humus," "Schlamm," and so forth. Consisting to a large extent of the dead remains of plants and animals, this material is rich in carbonaceous and nitrogenous substances in various stages of decomposition. The combustible organic matter may constitute as much as 50 percent of the total weight (Birge & Juday 1911; Black 1929; Juday, Birge, & Meloche 1941).

In some lakes and ponds the bottom may be further enriched by the deposition of various other organic substances. Griffiths (1936) considered the partially

disintegrated remains of an unusually abundant stand of Nuphar to be a factor of considerable importance in the lowering of dissolved oxygen in a certain ice-covered pool. It is probable that in Pasinski's Pond, in the present study, the rich growth of Anacharis and Spirogyra was at times sufficiently in a state of decay to use a large amount of oxygen.

At times water running into a lake, from fields or in inlet streams, may carry suspended material which settles to the bottom, adding to the organic load. If domestic sewage or other organic pollutional waste is allowed to enter a lake, it may form sludge deposits of great oxygen-consuming power. The danger of adding too much sewage or manure to winter carp ponds has been recognized by Knauth (1899), Sniezko (1941), and others. The likelihood of the formation of extensive sludge deposits in most natural lakes, however, is small, except in cases of out-and-out pollution.

The mechanics of the decomposition of bottom materials, and the part played therein by bacteria, has been the subject of considerable study. It is well known that bacteria in the bottom sediment are very numerous and diverse. Also, logically, these bacteria are adapted to the utilization of the bottom materials for their food. As is discussed below, many of these forms exist anaerobically, but there are many others which carry on aerobic decomposition when oxygen is available. Naturally, the activities of the bacteria are correlated with the temperature, but a large amount of decay goes on even at temperatures near freezing. Probably some sort of an adaptation may be assumed, since the bottom mud usually is relatively cold the year around.

The amount and nature of the bacterial decomposition depend also to a large extent upon the composition of the bottom deposits. Waksman (1941) divided the organic matter in lake bottoms into (1) readily decomposable constituents, such as carbohydrates and certain proteins, and (2) the more resistant "lake humus" components, such as lignins, and so forth. The organic matter on the bottom of dystrophic lakes has been shown (Henrici 1939) to be much less easily decomposed than that of eutrophic lakes.

ACTIVITIES OF GASES

An important part in the oxygen cycle is taken by the several gases which are generated during the processes of decay of organic matter. These gases, methane, carbon dioxide, hydrogen sulfide, ammonia, nitrogen, and possibly carbon monoxide and others, may be formed in the water, but are more apt to arise in large quantities from the decomposition of bottom muck. Their production comes about principally through the activities of anaerobic bacteria, which are present in the bottom materials in great numbers and many forms. Experiments have shown (Allgeier, Peterson, Juday, & Birge, 1932; Black 1929) that gas production by these organisms is very much slowed down at low temperatures. The former authors found the decomposition to be only about one-fifth as much at 7° C. as at 23°; Black obtained only

about a quarter as much gas from a sample kept at 4° C. as from one at room temperature. The gas produced at 4° was about half methane, the remainder being carbon dioxide, hydrogen, and nitrogen. It is obvious, furthermore, that the amount of anaerobic decomposition which takes place on the lake bottom is closely correlated with the kind and amount of organic material present, just as in the case of aerobic action, and that it may be much higher in sediments of a distinctly sludge-like nature.

The occurrence of these gases of decay in winter-bound lakes has been reported by several writers. Kochs (1891) spoke of the presence in winter carp ponds of methane, ammonia, and hydrogen sulfide, the last of which he believed to be an important agent of oxygen consumption. Under the extremely stagnant conditions found by Knauthe (1899) in a small pond, methane was so abundantly produced that "large bubbles of this harmful gas gathered in the middle of the pond under the ice and . . . the young people of the village found pleasure in boring holes in the ice, and burning the gas at the holes."

During the course of the present study gas evolution was noted many times. At the time of heavy fish mortality in Pasinski's Pond, in February, 1940, a very pronounced stench arose from holes chopped in the ice, the odor being at least in part that of hydrogen sulfide. In the same winter, the stagnant water of Richmond Lake also stank strongly for many days. Continuously throughout the entire period of ice cover (even during the comparatively mild winter of 1940-41), the water from the lower depths of Bog Lake reeked with hydrogen sulfide. The fact that the surface water usually was virtually free from this gas indicates that the gas either was oxidized before it reached the surface, or was held in chemical or physical combination in the lower water.

The possible harm to the fish caused by directly toxic properties of various gases is discussed below. The often more serious effect of these gases is the removal of dissolved oxygen from the water. This oxygen depletion may occur in two ways, by chemical or biochemical oxidation, or by the sweeping action of the gas in bubbling through the water.

Kusnetzow (1935) gave a rather strong argument for the theory that, in some lakes at least, the bacterial oxidation of methane and hydrogen arising from the bottom sediments may be the principal factor in the removal of oxygen from the water in the winter. In lakes in which the oxygen remained at high level throughout the winter he found the amount of methane and hydrogen coming from the bottom to be much less than in the "fish suffocation" lakes, although both types of lakes abounded in water bacteria. He concluded, therefore, that it is not alone the simple respiration of the bacteria, but rather their increased activity in the presence of methane and hydrogen, that exerts heavy demands upon the dissolved oxygen (to the purely chemical oxidation of these gases he attributed an insignificant part).

It is barely possible, of course, that Kusnetzow's

explanation may be somewhat in reverse, and that the increased production of methane and other reducing gases may appear as a result, rather than as a cause, of oxygen depletion, since lowered oxygen near the bottom would favor the activities of the anaerobic (gas-producing) bottom bacteria.

The purely mechanical action of gas bubbles in removing oxygen probably is of considerable significance at times (Welch 1935, p. 91; Knauthe 1899). The bubbles of gas may entrap oxygen and carry it to the surface, where it is lost to the atmosphere. The amount of oxygen so removed depends upon the number, size, and character of the gas bubbles, the temperature, and so forth. The last small fraction of the dissolved oxygen is harder to remove than that near or in excess of saturation.

DECAY OF SUSPENDED MATERIAL

Suspended particulate matter in lake water may arise from various sources, chief of which usually is the dead remains of plankton (for the purposes of this discussion living plankton is not termed "suspended"). It may contain also the remains of dead higher plants and animals. Naturally-formed detritus, and occasionally pollutional wastes, may be carried in by streams.

The quantity of material in suspension varies from lake to lake and from time to time, from an amount detectable only upon concentration, to that sufficient to render the water distinctly turbid. In general it is apt to be much greater in rich bodies of water than in those less eutrophic. It is sometimes cyclic, following cycles of plankton abundance.

This material varies in composition, but it is rich in organic matter. It is scarcely heavier than water, and sinks slowly. This probably is particularly true in the winter, not only because the water is slightly denser, but also because it has a greater viscosity at low temperatures (Welch 1935, p. 85). As a consequence of slow settling, the suspended organic material is in contact with the water for a fairly long time.

Since it contains a large proportion of organic substance, it is to be expected that the suspended material is capable of utilizing considerable oxygen. It seems that lake water usually contains large numbers of bacteria, although these numbers may decline somewhat in winter. Henrieci (1939) found in Lake Mendota that "under the ice in winter the bacteria are uniformly few in number until the bottom meter is reached, where they show an amazing increase." He pointed out, also, that bacteria in the water are for the most part periphytic, i.e., attached to suspended materials or to living plankton. Blue-green algae especially are collectors of bacteria (Henrieci & McCoy 1938). By this means the bacteria are given ready access to the dead plankton material.

The amount of bacterial action depends to a certain extent upon various physical and chemical factors, and upon the kinds of organic matter present. On the whole, the statement of ZoBell (1940) that plank-

ton remains are more readily oxidizable by bacteria than is the dissolved organic matter in the water, probably holds true. However, certain materials, such as chitin, lignin, and humus-like compounds, are less amenable to bacterial attack than the simple carbohydrates and proteins, and may reach the bottom unaltered. The semi-colloidal suspensoids of dystrophic lakes have been said to be relatively resistant to water bacteria.

Bacterial oxidation is of course slower at low temperatures than at higher ones. ZoBell obtained a Q_{10} for water bacteria of about 2.1, in the region 8°-25° C. Short-time (5-day) biochemical oxygen demand tests at 0° give correspondingly lower results than those at 20° (see discussion in the section on B.O.D.). It is of interest to note, however, that the eventual or ultimate B.O.D. may be fully as great at the low temperature as at the higher one.

Many opinions have been expressed regarding the relative importance of suspended material as an oxygen-depleting agent. Birge & Juday (1911, p. xiii), in defining the "zone of decomposition," stated that the dead materials settling into this zone are instrumental in oxygen utilization. Much evidence has been produced by various workers to substantiate this view. Rawson (1939) summarized the theory by saying that "there would seem to be greater possibility that the original explanation was the correct one, i.e., that hypolimnial consumption of oxygen is largely due to decomposition of dead plankton falling through the hypolimnion."

Divergent ideas, however, have been proposed by various writers, such as Drown (1892), Alsterberg (1927), Henrici (1939), and so forth. The theories of some of these workers, in assigning a larger share of the oxygen consumption to various other factors, have greatly minimized the part played by the decay of suspended matter.

Observations of the present investigation indicate rather strongly that, in the lakes studied, the suspended material played probably a large part in the oxygen diminution under the ice. For example, in Pasinski's Pond at times in the winter of 1940-41 the coincident occurrence of a large amount of suspended matter and of a very high oxygen demand (as measured by B.O.D. tests) was too marked to be casual. The argument is strengthened by the correlation observed between B.O.D. and the amount of suspended material at various depths. When the water near the surface was much more turbid with suspended matter than that near the bottom, it also had a much higher B.O.D.

DECAY OF DISSOLVED ORGANIC MATTER

It is difficult to distinguish, entirely, between dissolved and suspended materials, and therefore difficult to judge the relative oxygen-consuming powers. In practical work, distinction usually is made on the basis of passage through a high-speed centrifuge or a fine filter. The "dissolved" material so obtained may include a small proportion of substances which

are not true solutes, but very fine suspensoids or colloids.

Birge & Juday (1926) published the results of an extensive study of the organic content of several Wisconsin lakes. They found the amount of dissolved organic matter to be considerably higher in these inland lakes than in the sea, and usually to be several times as great as the amount of organic matter contained in the standing crop of plankton. The dissolved organic matter varied, in the several lakes, from about 6 to about 38 mg. per liter.

This material, according to Birge & Juday, is derived chiefly from plankton, although a small part of it may come from the disintegration of higher plants or from other sources. Its composition is complex, but it is relatively rich in various carbohydrates (only a small part of which, however, is sugars or other simple carbohydrates), and nitrogen in the form of peptides, amino acids, and so forth. Obviously these substances are capable of utilizing rather large quantities of dissolved oxygen (for example, the complete oxidation of only about 12 mg. of carbohydrate per liter would require all of the dissolved oxygen in water saturated at 4° C.). The extent of their oxidation, however, depends upon their suitability and availability as food for the water bacteria. On this question there has been considerable discussion. At least some of the dissolved substances, such as complex nitrogenous compounds, have been held to be very resistant to bacterial action (Krogh 1931, ZoBell 1940). Others, however, such as simple amino acids and carbohydrates, can more readily be utilized by the bacteria, the extent of such use depending upon numbers and kinds of bacteria present and the temperature. In the B.O.D. tests of this study no attempt was made to determine the proportion of the oxygen demand of the water which was due to the dissolved organic matter.

Although not classed as an organic substance, ferrous iron may be mentioned here as being a possible factor in dissolved oxygen reduction. Sometimes present in solution in certain lake waters, particularly of dystrophic lakes, it may, under the proper conditions, be converted into ferric iron, either chemically or biochemically, with the resultant consumption of oxygen. In certain brown-water lakes reported on by Brehm & Ruttner (1926), ferrous iron, of allochthonous origin, was said to exert a very high oxygen demand. In most clear-water lakes, however, probably this factor is a very minor one.

GROUND WATER AND SURFACE INFLOW

In certain lakes subterranean inflow may be of appreciable amount, even in winter. This ground water often is very low or totally deficient in dissolved oxygen, and it may thus reduce the oxygen content of the lake as a whole. Shopinzev (1940) held the large proportion of ground water in the Volga River, in the winter, responsible for the lowered oxygen content of the river. It is questionable, however, that ground water is a significant source of

oxygen reduction in most Michigan lakes in winter, for its flow usually is small.

Inflowing water arising from rain or melting snow or ice on the surface of the lake sometimes is lower in dissolved oxygen than is the water immediately under the ice, and hence upon mixing it may actually lower the oxygen content of the upper layer of water. The total body of water, however, is not affected to any considerable extent, since the inflowing water is comparatively small in volume, and usually carries some dissolved oxygen.

OXYGEN REPLENISHMENT

Once sealed in by a covering of ice, a lake cannot acquire oxygen, as in the summer, by wind agitation. Even the small blessing of surface diffusion is seriously restricted. Advantageously enough, a lake usually enters the winter period with its oxygen concentration at the normal annual maximum, i.e., saturation at 4° C., or about 13 p.p.m. In the deeper, more oligotrophic type of lake this initial oxygen supply may be adequate to carry the lake through the entire winter. But in shallow, organically rich lakes the processes of respiration and decay, discussed above, undoubtedly would consume the oxygen supply long before the end of winter, were that supply not somehow replenished.

Except for artificial aeration, and the ingress of oxygen-bearing water, augmentation of the oxygen supply can be brought about by only one means, photosynthesis. In many lakes, therefore, the maintenance under the ice of a copious oxygen supply is absolutely dependent upon the presence and activity of green plant life.

HIGHER PLANTS

The importance of rooted plants as oxygen producers in winter is not well known. The situation is complicated by great variations in the kinds and numbers of these plants which may be in an active state under the ice cover. Many observations have been made of rooted aquatic plants which were quite green under the ice, particularly in early winter before much snow had fallen. Olson (1932) stated that "higher aquatic plants in many instances die off in the fall. . . . There are a few plants, however, that remain active through the winter, and these can produce oxygen in considerable quantities when light is available." He reported the observation of green aquatic vegetation through the ice in late January, at which time the water in the immediate vicinity of the plants was supersaturated with oxygen. It is not especially uncommon for winter fishermen in spearing shanties on southern Michigan lakes to notice considerable rooted vegetation in a green condition. Early in the winter such plants as *Vallisneria* and certain pond-weeds may be quite actively vegetative.

However, for most of the higher plants (with particular reference to those inhabiting Michigan winter-kill lakes) winter is usually a time of little activity. With few exceptions, the lakes studied contained very little vegetation in a green condition in the winter.

Cattails, bulrushes, and water-lilies were brown at the onset of the ice; coontail, bladderwort, and most pond-weeds died down to a large extent soon after. The large beds of *Anacharis* which filled Pasinski's Pond were partially green at times, and may have contributed some oxygen to the water. Occasionally in Mud Lake and Green Lake a certain amount of green color was evident in some of the weeds, especially when the ice was bare. On the whole, however, the higher plants probably are a relatively insignificant source of oxygen in these lakes in the winter.

NON-PLANKTON ALGAE

Certain of the filamentous algae occasionally are found in abundance in the winter. It is fairly well established that many algae can thrive at low temperatures, given enough light. Smith (1933, p. 23) defines a group of algae, which he designates "winter annuals," which vegetate in the winter and fruit in early spring. This group includes one or two species of *Spirogyra*, as well as several single-celled algae. Knauthe (1899) attributed a part of the winter oxygen production in the ponds he studied to filamentous algae.

In Pasinski's Pond, in the winters 1939-40 and 1940-41, a very large mass of *Spirogyra* was present, especially in the south end of the pond. This material stayed green during a considerable part of each winter; its greenness varied with the amount of snow on the ice. The *Spirogyra* quite evidently had an appreciable effect upon the dissolved oxygen content of the water (see the section on dissolved oxygen in Pasinski's Pond). In none of the other bodies of water studied were non-plankton algae noted in any appreciable concentrations.

PHYTOPLANKTON

It has long been known that the microscopic plants of the plankton play an extremely important part in the replenishment of dissolved oxygen in lakes, even under the ice. Knauthe (1899) was well cognizant of the interrelations of light, an abundant crop of phytoplankton, and the production of oxygen in ponds in the winter. He found, at times, a very pronounced supersaturation of oxygen, coincident with intense activity of the plankton plants. Griffiths (1936) stated that the oxygen concentration in Long Pool, in February and early March, was "associated with a maximum abundance of phytoplankton, consisting mainly of *Dinobryon*, *Uroglenopsis*, and *Eudorina*."

Quantitative information concerning phytoplankton in ice-covered lakes is scarce. Trends of thought of various writers have indicated that (1) the phytoplankton as a whole diminishes in the winter months, (2) diatoms may become relatively abundant in winter at the expense of green and blue-green algae, and (3) there are apt to be large fluctuations from lake to lake and from winter to winter. Whereas some specific studies have been in agreement with these general ideas, other disagree. Kofoid (1903)

found that the Illinois River, as well as an inland lake, contained in the winter a relatively high amount of plankton, of which a fair proportion presumably was phytoplankton. Griffiths reported that, for Long Pool, phytoplankton was "even moderately abundant only during the colder months." In Lake Mendota, in 1916-17 (Birge & Juday 1922), the total phytoplankton was somewhat less in quantity in the winter than in the summer; *Microcystis* showed relatively little decline; *Aphanizomenon* reached a peak in early January and fell off sharply in late February; *Tabellaria* began to increase in late winter. The predominant plant of the nannoplankton in winter was *Aphanocapsa*, which was little changed from its summer concentration; in late winter *Chlorochromonas* began to appear in fair abundance.

In their survey of Green Bay, in 1938-39, Williamson et al. (1939) found the net plankton to be very small in amount throughout the entire period of ice cover, and to consist of a few diatoms and very little else. The ice was covered with snow for a large portion of the winter. The bloom of *Aphanizomenon* which had appeared in November was well dissipated by the time the ice had become solid in January.

In the present investigation no quantitative data regarding plankton were obtained. Nothing like a plankton bloom was observed at any time during the four winters. It is possible that there was considerable phytoplankton present at times, however, for many sudden and large increases of dissolved oxygen were recorded.

BACTERIA

Certain bacteria, such as the green and red sulfur bacteria, possess pigments somewhat related to chlorophyll, and are able to utilize light for photosynthesis. However, according to Van Niel (1935), who has made an extensive study of these photosynthetic bacteria, it is very doubtful that they produce any oxygen. The nature of their action is parallel to, rather than identical with, that of green plants. Carbon dioxide is reduced, but the necessary hydrogen is derived from organic substances or from H_2S , rather than from water.

Although these bacteria cannot properly be considered as direct producers of oxygen, they may have an indirect effect, in that they stabilize substances such as H_2S and CO_2 , and thus reduced the potential oxygen demand of the water. It is possible that these bacteria may exist and operate in lakes in the winter, particularly in lakes which contain hydrogen sulfide.

RUN-IN WATER

Inflowing water which arises from rain or melting snow or ice usually contains a few parts per million of dissolved oxygen, and may thus bolster a depleted oxygen content. This effect is often transitory, however, and is usually confined to the upper layers. Nevertheless, such incoming water probably helps occasionally to tide a lake over a perilous period, as perhaps occurred in some of the lakes under observation in 1937-38.

WINTER SUFFOCATION OF FISH

If the oxygen-replenishing agencies fail to produce oxygen as rapidly as it is being consumed, a serious shortage of dissolved oxygen may ensue, and the fish may be endangered. Certain things should be known concerning the suffocation of fish under the ice. How prevalent and how serious is winter-kill? What is the physiological basis for the death of the fish? What are the general consequences of winter-kill? What can be done to prevent it?

INCIDENCE OF WINTER-KILL

The extent of damage by winter suffocation may vary from the loss of only a few fish to the complete or almost complete annihilation of the fish population of a lake. The death of relatively small numbers of fish during any one winter probably indicates only an indirect connection with winter-kill. A certain number of fish succumb, during the winter, to disease, parasites, or accident. Birds are excluded from the water by the ice, and other scavengers are less active in the winter than in the summer; decomposition of fish carcasses proceeds more slowly at low temperatures; and thus quite a few fish which have died during the winter come to the attention of the casual observer at the time of the break-up of the ice.

There are records of the destruction by winter-kill of extremely large numbers of fish. In the mortality in the Racine River, Wisconsin (Hoy 1872) "thousands of barrels" of fish died. According to Olson (1932), 20,000 pounds of dead carp were removed in one day, in the winter of 1928-29, from a small lake in Minnesota. In Crystal Lake, near Gulfport, Illinois, over 80,000 pounds of fish, mostly carp and buffalo, were found dead at the end of the winter of 1939-40 (Illinois Natural History Survey, personal communication). At Georgetown Lake, Montana, in the winter of 1936-37, more than 700,00 trout are said to have perished (King 1937).

In Michigan, especially in such winters as that of the "big freeze-out," 1935-36, many severe fish losses have occurred. In the reports of various observers, references to "many hundreds," "thousands," and "large numbers" appear frequently. Cooper (unpublished report 1936) gave the following estimates of fish killed in certain lakes in southern Michigan, in 1935-36: Bateese Lake, over 200,000; Mud Lake, over 75,000; Green Lake, between 75,000 and 100,000; and Park Lake, over 150,000.

Again in the winter of 1944-45, several lakes in Michigan, as well as in Wisconsin and Minnesota, suffered extremely large winter-kill losses.

Complete destruction of a fish population apparently is very rare. It has been recorded by Knauth (1899) for a carp pond, but this was an artificial situation. In Pasinski's Pond, in 1939-40, the bluegills were all killed, but most of the bullheads survived. This pond is scarcely typical of southern Michigan lakes, being small and exceedingly rich in organic matter. No other substantiated record of a complete winter-kill of fish in Michigan waters exists.

On the other hand, many lakes which were thought at the time to be entirely killed out have later been found to contain a surviving stock. It is difficult to be certain whether the fish have all been killed in some lakes, because of stream connections through which fish might enter following the kill.

PHYSIOLOGICAL ASPECTS

CAUSE OF DEATH

Mention has been made, in the introduction, of the theories and beliefs of various writers as to the *modus operandi* of winter-kill. Although certain of these writers have blamed such factors as "poisonous" gases (presumably hydrogen sulfide, ammonia, or methane), the weight of majority opinion has placed the responsibility on lowered dissolved oxygen tension. This theory has been fairly well substantiated in the literature.

The present survey presents still more evidence in the same direction. Wholesale death in Pasinski's Pond occurred at the only time during the three winters of investigation there that the dissolved oxygen in the pond fell to 1 p.p.m. or less for several consecutive days. Similarly, at other lakes substantial fish mortality has been found to come about at times of extremely low oxygen. This was found to be the case also during the studies made by the Institute for Fisheries Research in the severe winter 1935-36.

However, it must be remembered that almost invariably low dissolved oxygen concentrations under the ice are accompanied by various other adverse conditions. The very processes of decay which consume the oxygen produce, at the same time, carbon dioxide, methane, hydrogen sulfide, and possibly ammonia. Hence any conclusion, *a priori*, that lack of oxygen is indisputably the sole cause of death is unjustified. Complete knowledge must rest on physiological experiments, because the several factors cannot readily be disentangled in nature.

The reasoning is speculative. It is axiomatic that fish die if the oxygen tension remains for any considerable time below a minimum value. But it also is true that the various noxious gases named above, if present in sufficient quantity, can be fatal to fish. Carbon dioxide alone, in high concentration, can kill fish, even in the presence of abundant oxygen. Furthermore, there are complex relationships. To take a common example, the presence of large amounts of carbon dioxide greatly reduces the ability of fish to utilize oxygen at low tensions (Fry 1939, and others). In other words, the toxicity of carbon dioxide increases with lowered oxygen tension.

The literature on winter mortality of fish has insufficient information on which to base any definite conclusions regarding the relative importance of these various factors. Nor do the data of this study give rise to any completely satisfactory deductions. In general, the CO_2 concentrations, although appreciable, were not alarmingly high, and the increase was somewhat gradual (a point apparently of some significance, as discussed below). It is probable that,

compared to the dissolved oxygen at its lowest levels, the carbon dioxide was not the most dangerous factor. Also, although the evidence at hand is scant, it appears possible that the amounts of hydrogen sulfide and other poisonous gases which usually were present in the lakes studied were not in excess of the tolerance limits of the fish.

Further speculation is fruitless. Suffice it to state that very low dissolved oxygen concentrations are probably the primary cause of death of fish in winter-kill, and that the effects of low oxygen may be augmented by the presence of carbon dioxide, and often of other harmful gases.

TOLERANCES AND ADAPTATIONS

In laboratory determinations of low oxygen tolerance limits of fresh-water fishes, most workers have neglected the lower temperature ranges. Even the experiments at room temperatures, of which there have been many, have produced results in considerable conflict, depending upon experimental method, species of fish, and the effect of various uncontrolled conditions.

Refining and extending a method of field observation used by Smith (1925), Moore (1942) obtained some figures for low-temperature oxygen requirements, that apparently are rather dependable. The experimental fish were held in live boxes in natural waters of various oxygen tensions, and the results are stated in terms of survival or non-survival for a 48-hour period. Control was good, and the effects of handling, pH, and CO_2 probably were minimal. It was found that the "thresholds of many species of fresh-water fishes lie between 1.0 and 2.0 p.p.m. However, some of the less tolerant species may require up to 3.0 p.p.m. or possibly higher." Even at extremely low oxygen concentrations, death did not occur immediately (in some instances not in four hours), indicating that suffocation at low temperatures requires a comparatively long time.

Moore's figures confirm rather well the conclusion of Thompson (1925) that, at low temperatures, "dissolved oxygen concentrations between zero and two parts per million will kill all kinds of fishes." Data of the present investigation are entirely inadequate to establish tolerance limits. However, at certain times, dissolved oxygen concentrations of less than 2 p.p.m. were found, with the apparent survival of the fish. For instance, in Pasinski's Pond in February and March, 1940, some 20 stations were sampled regularly, assuring fairly adequate coverage of the four acres. For the consecutive sampling dates February 26, 28, and March 1, not one dissolved oxygen value of over 1.5 p.p.m. was found at these stations, and most of the values ranged from 0.0 to 1.0 p.p.m. Although the bluegills died, most of the population of the more hardy bullheads lived.

Carbon dioxide tolerances of fishes have been studied by many writers, such as Wells (1918), Powers and associates (Powers 1938, and other papers), and Black and his associates (Irving, Black, & Saford 1941; Fry 1939; etc.). Powers has concluded

that fish can satisfactorily absorb oxygen in the presence of carbon dioxide in the concentrations usually found in nature. The factor which in his opinion often causes mortality is a sudden increase in CO_2 , to which the fish cannot adjust themselves. No special reference is made to the conditions of winter, when abnormally high carbon dioxide tensions may occur.

It has been claimed that fish exhibit avoiding reactions toward low dissolved oxygen (Thompson 1925) and toward high carbon dioxide (Wells 1918). However, it was observed many times in this study that when an open hole is maintained in the ice, at times of low oxygen in the water, the fish will crowd into the open hole, and will remain there until they succumb, even though the oxygen drops to zero while nearby water still contains oxygen. For example, in Richmond Lake on February 18, 1940, the surface water in an open hole contained only 0.4 p.p.m. of dissolved oxygen, while that at a station not far away had 1.9 p.p.m. Yet the hole was full of dead and dying fish. Similarly, in Pasinski's Pond, on February 19, 1940, there were hundreds of dying fish in the open hole, and at the same time the oxygen at a station only 40 feet away was 2.8 p.p.m. It is possible that the avoidance reactions of the fish are relatively slight at such low temperatures. Also, it seems likely that the tendency for the fish to move into an open hole and stay there is conditioned by a positive reaction toward light or toward open water, or by the opportunity to gulp air at the surface.

It is known that there are considerable differences in the sensitivity of various species of fish to adverse conditions. Various listings of the order of resistance have been given. Fry (1939) listed them on the basis of the effect of carbon dioxide on oxygen utilization. Moore (1942) gave the order in which several species resisted diminished oxygen tension at low temperature. Almost all authors agree that in general such species as sunfish, yellow perch, and black bass are more sensitive to lowered oxygen tension and other adverse conditions than those species commonly called rough fish, such as bullheads, carp, and dogfish. It is probable that within species there are relatively tolerant and relatively susceptible physiological races, and that hereditary individual differences exist within single populations.

Differences in sensitivity also exist because of differences in age, physiological condition, and (possibly) sex. Moore concluded that older fish can withstand winter oxygen depletion better than can younger ones, since the metabolic rate decreases with increasing age. Fish in poor physiological condition, or those weakened by injury, parasites, or disease no doubt become victims of winter-kill more readily than the more hardy individuals.

Certain fish species have been shown to have special physiological adaptations which enable them to survive conditions that otherwise might be catastrophic. An example is the mud minnow (*Umbra*). This fish is the only species known to be present in Bog Lake, where it has maintained itself through

countless winters (the stock could not have been replaced by immigration in recent decades, for the lake has no water connections). During many of these winters, the lake must have been completely devoid of oxygen for considerable periods, yet the mud minnows survived. The explanation probably lies in the ability of this fish to utilize atmospheric oxygen. It has been demonstrated (Geyer & Mann 1939, and others) that *Umbra* can exist in water of low oxygen concentration if it is allowed access to the surface, in order to gulp air. It is not very clear just how the fish can obtain air in the presence of an ice cover, but it is possible that cracks in the ice, and air pockets under the ice, allow enough contact with the atmosphere to fulfill the relatively small needs of the fish in cold water. Perhaps there is a possibility that the mud minnow may undergo actual hibernation, perhaps buried in the muck of the bottom, for part or all of the winter, although Morgan (1939, p. 321) has raised the question of the existence of true winter dormancy in fishes. At any rate, a very sluggish fish would consume very little oxygen.

CONSEQUENCES

Heavy winter-kill in a lake may reduce the fish population to such an extent that fishing for the next season or two is very unproductive. Unfortunately, no really quantitative records are available for Michigan lakes regarding the fishing success in the first and second summers following a heavy winter mortality. In fact, the knowledge that a lake has suffered a large loss often keeps most fishermen away from that lake for a year or two, and hence a creel census would be of small value.

Within a certain range, the effect upon the fishing is more or less in proportion to the extent of the kill of the game fish. However, in some lakes, and with a not too heavy loss, a different and perhaps even desirable result may obtain. It is known that many Michigan lakes are over-populated with various game fish to the extent that extreme stunting occurs. It is altogether probable that a considerable reduction in numbers of these fish results in faster growth of the remainder, and hence in fewer, but larger, fish becoming available to the angler (Beekman 1941, 1943).

It appears likely that, following a winter-kill, the fish population recovers to a large degree within a very few years, and eventually becomes restabilized at its original level. Rebuilding of the population may be effected by artificial stocking, by immigration through connecting streams, or by the fecundity of a surviving parent stock. An apparently well substantiated instance of a recovery from a surviving stock is that of Goose Lake, in Jackson County. This lake was considered good fishing for largemouth bass. It was hit severely by winter-kill in 1935-36, when it was popularly supposed to have been almost entirely depopulated of fish. Natural reinvasion could not take place because the lake has neither inlet nor outlet, and there were no recorded artificial plantings

of bass between 1936 and 1941. Fishing conditions in the lake after the spring of 1936 have been described by Haines (1941). Although admittedly based on a small amount of observation, his information is of interest. In 1938, two years after the winter-kill, he found that fishing was still rather poor, and that the bass taken were small. But in 1941, after a total of five years, he made several good catches of large bass.

Species differences in tolerance of fishes to unfavorable conditions often brings about a differential winter-kill. In general the game fish are more sensitive than are the rough fish, and several reports in the literature have indicated that the game fish suffer more damage than the non-game species. As already mentioned, the winter-kill of 1939-40 killed all the bluegills in Pasinski's Pond, but destroyed relatively few bullheads. An apparent exception to this general rule was found by Aitken (1938), who reported, "Although many fish died the winter of 1936 they were mostly carp, buffalo, and sheepshead whose loss was probably beneficial to the lakes."

Reports made by fishermen and other interested persons probably are influenced by the propensity of the observer toward noticing game fish, his tendency to neglect to observe minnows and other small fish, and at times his inability to recognize other than the game species. Nevertheless, the figures available, as regards winter-kill in Michigan lakes, distinctly show the game species to be the ones most affected. As Smith (1941) and others have pointed out, this discrimination has the effect of leaving a population, and a brood stock, composed of a large proportion of rough fish. In this manner the species balance between predator fish, game and food fish, and forage fish may be seriously disrupted. It may well be, however, that this balance becomes restored, through the workings of ecological forces, within a relatively few years.

Various other animals besides fish sometimes are victims of winter-kill. Kochs (1891) reported the death of very large numbers of frogs. Olson (1932) also stated that frogs are subject to winter suffocation. In the present investigation, dead tadpoles were observed a few times, but never any dead adult frogs, nor are frogs specifically mentioned in the reports of winter-kill in Michigan lakes.

Many dead snails were observed after the breakup of the ice, particularly in Green Lake, but it is not known whether they were killed by low oxygen or died from other causes. Similarly, although a few dead mussels, crayfish, and turtles may be seen along the shore of a lake after the ice melts, it is questionable that they are the victims of winter-kill, since their death in large numbers has seldom been reported.

The plankton invertebrates probably are destroyed in large numbers in some waters. Kofoid (1903) recorded the "practical extinction of the plankton" in places in the Illinois River during a winter of heavy fish mortality. However, since many of the plankton animals normally are subject to vast changes in num-

bers, cyclic or otherwise, and are equipped to weather adverse conditions by means of winter eggs or other resistant forms, it is likely that winter-kill is by no means a complete catastrophe to them. Benthic invertebrates, such as aquatic insect larvae and nymphs, no doubt are affected to some extent.

PREVENTIVE AND REMEDIAL MEASURES

Lake conditions conducive to winter-kill are more fitly subject to prevention than to cure. Once a lake develops an oxygen deficiency to the point where fish are in distress, it is doubtful if artificial means can avert considerable destruction. On the other hand, there are certain measures which, if applied early enough in the winter, may go far toward preventing harmful conditions from arising. In the following discussion not only are these methods considered, along with the extent of their economic feasibility, but also brief attention is given to sundry procedures, proposed or even actually attempted by various workers, which are neither theoretically nor practically sound.

FLOWING WATER

If an appreciable flow of water through a lake can be maintained throughout the winter, and if the inflowing water always carries a reasonably large amount of dissolved oxygen, it is logical to suppose that the water of the lake, at least within the path of flow, can be kept supplied with oxygen. Mud Lake furnishes an example of a stream's having considerable influence upon the oxygen content of the lake water. Hubbs & Eschmeyer (1938) discussed the possibility of diverting a natural stream into a lake in order to prevent winter-kill. However, it will generally be impractical to bring about such a diversion. Furthermore, there is not always assurance that the stream will remain aerated, since it in turn may arise in another lake where low oxygen also prevails.

Water from wells perhaps may be utilized as a source of supply for some ponds, but as a rule ground water contains little oxygen and therefore must be artificially aerated before it enters the pond. The results of an experimental use of such a water supply at Pasinski's Pond, discussed above, showed little if any improvement in conditions which could be attributed to the well water, presumably because the supply of oxygen it brought in was insufficient to overcome the large oxygen demand which existed in the pond.

RAISED WATER LEVELS

Smith (1941), Hubbs & Eschmeyer, and others have recommended raising the lake level as a means of preventing winter-kill by enlarging the initial supply of oxygen. Probably it is feasible to raise the water level of some shallow lakes by a foot or two in the fall or early winter; whether this additional amount of water can furnish enough oxygen to meet the demands of decaying organic material is doubtful. As discussed above, it seems likely that the average shallow lake of the winter-kill type uses, during a

long winter, more than the amount of oxygen with which it starts the winter, the balance being made up by photosynthetic production under the ice.

HOLES IN THE ICE

For no one knows how many decades, fishermen, conservationists, and others have attempted to relieve winter suffocation by cutting holes in the ice. Even scientific writers have recommended the procedure (Wickliff n.d., and others). Presumably these workers subconsciously postulate some such analogy as lifting the trap-door to a dungeon, thus to allow its occupants access to air and to life. Or there may be present the notion, expressed in a newspaper account (Milwaukee Sentinel 1939), that holes in the ice will "allow the poisonous gases which mean death to the fish to escape." At any rate, despite many published statements in deprecation (Knauthe 1899, Hubbs & Eschmeyer 1938, Milwaukee Journal 1939, Smith 1941, and others), the practice still has many ardent followers.

The seal of an ice cover is not nearly so perfect as is often supposed. Cracks, pinholes, and air-pockets would relieve any very great pressure that a dissolved gas might build up, and allow the escape of the gas. The very fact that almost invariably the greatest concentrations of methane, hydrogen sulfide, and carbon dioxide are near the bottom rather than near the surface would indicate that it is not the mere presence of ice that prevents their escape from the water.

In the absence of agitation, diffusion of air through the surface film of water is exceedingly slow and small in amount. Any appreciable aeration of the water of a lake by mere contact with the air over the area of a number of holes in the ice is impossible. It is true that if agitation can be accomplished, as by wind, much air can be put into the water. But, as those who have tried it know, the task of removing the ice from any appreciable area of the water is a large one indeed (to clear one acre of ice one foot thick would require the removal of 1,100 tons of ice). Artificial agitation, by outboard motors or other propeller devices, unless used in impractical numbers, cannot affect a large enough proportion of the lake's volume to be of any significant aid.

A popular theory is that fish are benefited by coming to the surface at open holes and gulping air. However, most fish are fitted primarily to extract their oxygen from that dissolved in the water, and are poorly equipped to utilize atmospheric oxygen. It is held by Powers (Powers, Shields, & Hickman 1939, and other papers) that gulping may actually be detrimental, because it brings about rapid changes in carbon dioxide tension.

Holes cut in the ice may result in actual harm because of their attraction for fish. As described above, fish tend to congregate at an open hole, and may remain there until conditions in that immediate place become fatal to them, even though there is better water not far away.

ARTIFICIAL AERATION

Various experiments, in Michigan and elsewhere, in the artificial aeration of ice-bound lakes by means of water or air pumps have been described above, in the section on Experimental Studies. Almost all of these experimenters have reached the conclusion that pumping methods are wholly inadequate to aerate even a fair-sized body of water.

The difficulty with almost any pumping method is in getting aeration for any appreciable distance from the seat of operations. Furthermore, the effects of the pumping usually are quite transitory.

Perhaps the possibilities of pumping have not entirely been exhausted, and further experimentation may be justified. It is possible that efficient air or water pumping over a long period of time could introduce considerable oxygen into a very small body of water, such as a farm pond. Certain precautions should be used, for instance to avoid stirring up bottom materials and thus making them more readily available for bacterial oxidation (Hubbs & Eschmeyer 1938). Pumping would have more chance of being effective if started prior to the attainment of extremely bad conditions, rather than after the oxygen is well exhausted. After the water has developed a large oxygen demand, the small amounts of oxygen that are added are quickly consumed. There seems to be little hope that pumping methods will ever be found to be feasible for larger bodies of water.

CHANGES IN VEGETATION

Since aquatic vegetation is known to be a producer of oxygen, under the proper conditions, it has been proposed (Aitken 1938) that winter aeration of lakes could be accomplished by increasing the amount of vegetation present. As has been pointed out above, the higher plants usually are responsible for relatively little oxygen production during the winter. During periods of snow cover, there is little photosynthesis, and the dead remains of plants may become an agent of oxygen consumption. It is therefore doubtful that any aid in alleviating winter suffocation is to be derived from the artificial propagation of plants.

Plankton plants can be increased by the addition of fertilizer to the water, but excess fertilizer, and the remains of plankton algae that die, have a large demand for oxygen. The balance, therefore, is so delicate that tampering is not justified in the light of the present knowledge concerning artificial fertilization of lakes.

In extremely weedy lakes, it is perhaps more desirable from the standpoint of winter-kill prevention to decrease, rather than increase, the amount of rooted vegetation, since the winter decay of water weeds may use part of the oxygen supply. However, the removal of rooted vegetation from a lake presents many difficulties, and probably should not be considered as an economically sound method.

SNOW REMOVAL

It has been pointed out (in the section on Light Penetration) that there is a definite relationship between the amount of light penetrating the snow and ice cover and the dissolved oxygen content of the water. The presence or absence of a long-continued snow cover on a lake can mean the difference between safety and doom for the fish. It is therefore apparent, and has been mentioned by several authors (Hubbs & Eschmeyer 1938, Smith 1941, and others), that by far the best single method of preventing winter-kill, from a theoretical viewpoint, is the removal of snow from the ice. Moreover, such removal should not wait until dangerous conditions develop, but should be carried out regularly after each major snowfall.

Practically, the method offers many difficulties. Large-scale snow scraping entails the use of power machinery, which is rather costly, and which requires fairly heavy ice for safe operation. Hand shovelling is extremely slow and laborious. There may be merit in such schemes as that of using road-scraping machinery at times when it otherwise would be idle, or that of making a community project out of clearing the ice of snow for the additional purpose of providing skating. Furthermore, the effort could be somewhat lessened by clearing only strips, with alternating windrows of piled-up snow (which might, however, be scattered back onto the cleared areas by subsequent winds). On the whole it is likely that, although the method may be feasible for relatively small bodies of water, it could not be applied to all of the large winter-kill lakes of southern Michigan.

As discussed above, there is considerable promise in the method of removing snow by means of a stream of water, pumped from under the ice. The snow need not be thoroughly melted; it has only to be wet down into a slush. Upon refreezing, it forms a layer of rough ice, which although rather cloudy nevertheless is much less opaque to the light's rays than is snow. The feasibility of applying this method to any considerable area has not yet been determined, but the possibilities seem to warrant further experimental application.

FISH REMOVAL

The removal of fish from a lake subject to winter-kill may be directed toward accomplishing one of two objects. The effect sought may be the diminution of the oxygen demands of the fish by removing a part of them, as in the experiment described by Olson (1932), in which 160,000 pounds of carp were removed from a small lake in the (vain) hope of saving the game fish. As discussed above, the oxygen consumption by fish probably is a very small part of the total oxygen utilization in the water under the ice, and hence the removal of part of the fish will have comparatively little effect in maintaining the oxygen supply.

Smith (1941) discussed the removal of fish (presumably game fish) for another purpose, that of taking them from the danger of winter-kill, and trans-

ferring them to deeper lakes where they will be safe. This procedure is a logical one, and in many instances when the threat of disaster is imminent, it may be an advisable thing to do. However, rescue operations in the winter are difficult and costly, and should be considered only as an emergency measure.

SUMMARY AND CONCLUSIONS

In the past, comparatively few studies have been made of winter conditions in lakes, largely because of the difficulties of winter field work. There are, however, many limnological aspects of lakes in winter which are worthy of observation. A cover of ice and snow brings about striking changes in the water. By interfering not only with gaseous exchange, but also with photosynthesis, this cover may have a great effect on the dissolved gases of the water, particularly on the oxygen balance. Among the disasters which may occur when this balance is adversely upset, the most dramatic and economically most important is the destruction of fish by suffocation.

Winter-kill of fish has been recorded many times in the last half-century, in Europe as well as in North America. In this country it is of more or less common occurrence in several north central states. In Michigan, it has occurred in many lakes (though in a relatively small proportion of all of the lakes of the state). There have been kills in many winters, the most notable of which, in recent years, were those of 1935-36 and 1944-45, during which untold hundreds of thousands of fish perished.

The dissolved oxygen content of the water under the ice furnishes a usable and reliable index to chemical conditions related to the well being of the fish. The oxygen concentration varies, sometimes abruptly, throughout the winter and from one winter to another. The greatest and most sudden fluctuations occur in shallow, extremely eutrophic lakes. The dissolved oxygen in a deeper, less eutrophic lake was found to remain remarkably constant throughout the period of ice cover. In respect to dissolved oxygen, a small pot-hole bog lake showed even greater extremes than shallow hard-water lakes.

Of the four winters of the investigation, in only that of 1939-40 did serious conditions develop in the lakes under observation. During that winter the ice was covered with snow for a comparatively long time. In the winters of 1937-38 and 1940-41 snow coverage was of short and irregular duration. In 1942-43 a heavy snow blanket was present for three or four weeks early in the winter, but was dissipated in time to avert the development of dangerous conditions.

Changes in oxygen concentrations, even from week to week, were definitely correlated with changes in the depth of snow on the ice. Measurements of light intensities showed that only a very small amount of light penetrates through even a few inches of snow. Unquestionably a foot or more of dry snow transmits too little light to actuate photosynthesis. On the other hand, ice, even though it is cloudy, permits the penetration of considerable light.

It is probable that the respiration of fish, other animals, and plants plays an insignificant part in the depletion of the oxygen. The main oxygen consumption comes about through the bacterial decay of organic matter, which is largely derived from dead plankton, and is either suspended or dissolved in the water or lies in the form of a mucky deposit on the lake bottom. This bottom deposit also may act indirectly to utilize oxygen, through the anaerobic production of methane and other reducing gases, which in turn are oxidized in the water. The relative importance of each of these organic materials in oxygen utilization is not known, but the correlation of oxygen depletion with general organic richness of the lake is clear-cut. Oxygen consumption is a continuous process throughout the winter, but may be subject to some degree of influence by changes in conditions of temperature and light.

Opposed to oxygen depletion is its production by photosynthesis. In this production, in winter, higher plants are involved to only a minor extent; the chief oxygen output is that of the phytoplankton. The amount of photosynthesis varies greatly, in accordance with the amount of light which penetrates the ice and snow cover.

Winter-kill of fish is principally a matter of suffocation caused by a lack of sufficient dissolved oxygen. High concentrations of carbon dioxide or other harmful gases are contributing factors. The oxygen requirements of fish are comparatively low at low temperatures; but nevertheless certain minimal oxygen thresholds exist beneath which fish cannot indefinitely survive. Different species show differences in tolerance, and hence differential kills occur.

The mortality varies from that of a few fish to the destruction of almost the entire population. Total kill is rare; and, when a residue fish stock is spared, recovery by natural propagation probably is largely completed within a few years, provided a second kill does not occur meanwhile. The detrimental effect upon fishing may be great for the first year or so, however, and the reputation of the lake for fishing is likely to suffer. The effects of winter-kill may not always be altogether deleterious, however, for the thinning of a large and stunted population may result in increased growth of the surviving fish. A heavy winter-kill may tend to disrupt the species balance, by differentially killing the more sensitive species.

Once a lake has developed intense winter stagnation, usually little relief can be secured from the application of artificial measures. Cutting holes in the ice does virtually no good, because air cannot enter the water, by diffusion alone, in any appreciable quantity. These holes may even be harmful, because fish tend to congregate in an open hole and hence to deplete the oxygen in that immediate locality. Nearly all pumping procedures have been found not to be feasible, especially if large bodies of water are involved.

Both theoretical considerations and the results of

experimentation indicate snow removal to be a logical and perhaps feasible method for the prevention of winter-kill. The economic practicability of the method is still largely unknown. For small lakes, particularly those which are important fishing waters, it holds considerable promise.

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INJURY AND DEATH OR RECOVERY OF TREES IN PRAIRIE CLIMATE

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INJURY AND DEATH OR RECOVERY OF TREES IN PRAIRIE CLIMATE

INTRODUCTION

Several years of decreasing precipitation initiated the 7 years of drought. By midsummer of 1934 it was clear that the prairie region of the Middle West was undergoing the greatest drought since the beginning of its recorded weather history. The 12 months following June, 1933, was the driest weather period ever recorded not only for the Dakotas, Minnesota, Nebraska, Iowa, Illinois, and Missouri, but also drought in Kansas, Oklahoma, and Colorado was very severe (Kincer 1934). This intensely dry period, as well as those in several of the following years, was accompanied by record-breaking temperatures, extremely low humidities, and exceptionally high rates of evaporation. These were the years also of high winds, swarms of grasshoppers, and great dust storms.

Great losses were suffered by native trees both along the western margin of woodland and within the area of climax deciduous forest. Where post-climax forest extends far westward along rivers and streams into the semihumid and dry grassland climates, losses were extremely heavy (Fig. 1). These losses occurred during the past decade of drought despite the fact that in the prairie area and especially west of the Missouri River the more mesic species of trees are not found and only the more drought resistant kinds occur. Compensations for low water content of soil, high wind, and low humidity supplied by rivers and streams were often inadequate.



FIG. 1. Loss of elms by drought along the Weeping Water River in eastern Nebraska. They were growing on the flood plain and were protected from drying south winds by a steep bluff. Photo in May, 1944, showing some recovery. (Unless otherwise indicated all photographs are by the authors.)

FORESTS AND TREES IN PRAIRIE CLIMATE

It has been estimated that 15 percent of Iowa, owing to its many large rivers and network of

streams, was forested. Perhaps nearly the same conditions occurred in the similar climate which prevailed over the prairies of Missouri. But only 2.5 to 3 percent of the area of Kansas and Nebraska was native forest. Along the Missouri River a strip of forest extends westward and northward from the main forested area to northeastern Kansas. It narrows rapidly where it extends farther northwestward in Iowa and Nebraska.

EFFECTS OF DRIER CLIMATE NORTHWARD AND WESTWARD

Decrease in area occupied by woody vegetation, decrease in number of species, dwarfing in size of individuals, and their confinement to the most favorable sites, are all well illustrated along the Missouri River in eastern Nebraska. The data are from Aikman's study of these forests (1929). In the south-

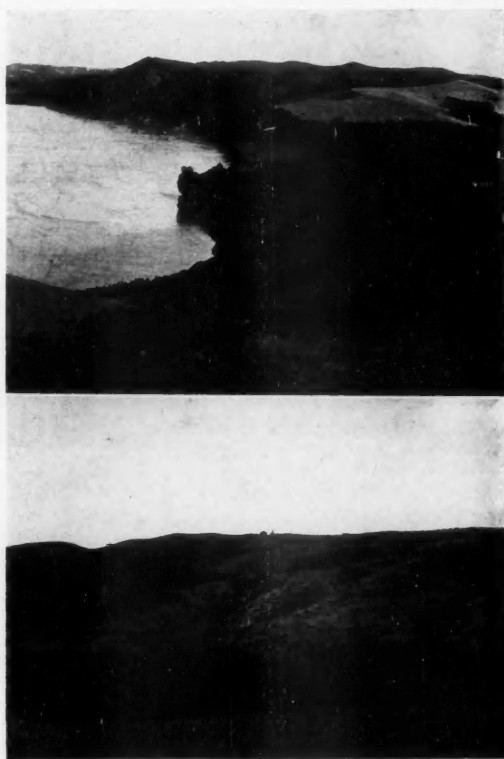


FIG. 2. (UPPER) Wooded north-facing bluff on the Missouri River and trees along a ravine, 25 miles west of Yankton, South Dakota. (LOWER) The south-facing slope of a similar bluff with patches of rough-leaved dogwood (*Cornus asperifolia*), coralberry and snowberry (species of *Symphoricarpos*), and smooth sumac (*Rhus glabra*). Bur oak (*Quercus macrocarpa*) occurs in the ravines.

east under an annual precipitation of 33 inches, the average width, in Nebraska, of the general potential forest area, which is dominated only in the more protected parts by red oak (*Quercus borealis maxima*)¹ and linden (*Tilia americana*), is about 25 miles. But in northeastern Nebraska under 28 inches of precipitation it is only 2.5 miles. The height of the trees in the best situations southeastward is 80 to 90 feet, but this decreases to an average height of 25 feet in the northwestern part of the area. Still farther northwestward, where red oak does not extend and the precipitation is only 22 to 23 inches, linden was found only on the side of the bluff, the north-facing slope, next to the river (Figs. 2 and 3).



FIG. 3. Forest of red oak (*Quercus borealis maxima*) and linden (*Tilia americana*) in southeastern Nebraska extending over hills and valleys several miles back from the Missouri River.

In the bur oak (*Quercus macrocarpa*) community, which occupied the tension zone between prairie or shrubs and the more mesophytic trees, the average height of the trees was reduced from 70 feet in southeastern Nebraska to 20 feet under a precipitation of 23 inches. The total number of upland, woody species of ecological importance was 62 in the southeast but only 31 in the northwest. The number of flood plain species was likewise reduced from 16 to 12 (Fig. 4).

Studies by Weaver, Hanson, and Aikman (1925) along certain streams flowing eastward into the Missouri River have added information regarding distribution of trees and communities of trees according to sites afforded by the stream and the ability of various species to tolerate adverse climatic conditions. For along these streams in prairie the balance between forest and grassland is so delicate that a little higher water content of soil, a slightly greater humidity, or protection from drying winds throws this balance in favor of tree growth, while the reverse conditions exclude it. Pioneer trees at the stream sources are those with light, windblown seeds, such as willows, cottonwood, elms, boxelder, and ash. Farther down stream, where a flood plain with portecting banks occurs, trees appear which spring from large rodent-carried fruits, such as black walnut (*Juglans nigra*), bur oak, and honey locust (*Gleditsia triacan-*

thos). At first the trees may occur in mixture—willows (*Salix amygdaloides*, *S. nigra*, and others), boxelder (*Acer negundo*), elms (*Ulmus americana* and *U. fulva*), walnut, oak, and hickory (*Carya cordiformis*)—all in the one undiversified habitat, the irregular flood plain. Still farther down stream, however, where the creek has deepened its channel and there is a lower flood plain subject to overflow, a higher flood plain or terrace, and sloping banks and bluffs, the trees are promptly grouped into definite communities. The intolerant willows largely disappear, boxelders clothe the lower flood plain; green and white ash (*Fraxinus pennsylvanica lanceolata* and *F. americana*), elms, and walnut cover the upper one; and oaks and hickories are found on the higher ground. Thus, a stream course cutting deep canyons has both the most diversified habitats and the largest number of communities of trees.

The more favorable climate for tree growth in southeastern Nebraska and eastern Kansas is indicated not only by the larger number of species present, but also by their greater development both in diameter and height (Fig. 5). Here they are found on hilltops as well as on hillsides and in the valleys. But as one travels westward, very soon the natural occurrence of trees is confined largely to flood plains, bluffs, and ravines. The decreasing precipitation



FIG. 4. View of flood plain forest near Nehawka, in eastern Nebraska, at the base of a steep north-facing slope. The trees are hackberry (*Celtis occidentalis*), American elm (*Ulmus americana*), red elm (*U. fulva*), green ash (*Fraxinus pennsylvanica lanceolata*), and Kentucky coffeetree (*Gymnocladus dioica*). One very old hackberry, not shown here, was over 4.1 feet in diameter and 95 feet tall.

¹ Scientific names of trees and shrubs are according to Kelsey and Dayton, Standardized Plant Names; those of other plants Britton and Brown's Illustrated Flora.



FIG. 5. American elm and other trees of a well developed flood plain community on the Big Nemaha River near Falls City, Nebraska. The tree in the foreground is 3.5 feet in diameter and 95 feet high.

westward, approximately an inch for each 25 miles along the eastern part of the Kansas-Nebraska border, and increasing evaporation are clearly recorded in rate of growth. The average rate of diameter growth of green ash on the flood plain of the Missouri River was found to be an inch in 3.1 years. On the upland the time interval increased to 5.2 years 40 miles westward, then to 6.8 years 55 miles farther west, and finally to 7.4 years 143 miles west of the first station. This decrease to one-half in rate of growth of ash was exceeded by that of the cottonwood (*Populus sargentii*), which required only 1.1 years per inch diameter increment near the river but 3.4 years 143 miles westward (Aikman 1929).

FOREST COMMUNITIES AND TREES IN TRUE AND MIXED PRAIRIE

Only a few species of woody plants occur along the streams of central Nebraska and Kansas, and these are noticeably smaller in every way than those in the eastern portion of these states (Fig. 6). A height of 20 to 35 feet is common, and the deciduous trees are often confined to the lower banks of the streams. The lower branches usually occur only 5 to 10 feet above the soil, depending largely upon the degree of protection from winds. The drought-enduring deciduous species that grow in western Nebraska and Kansas are even fewer and smaller. They are restricted to

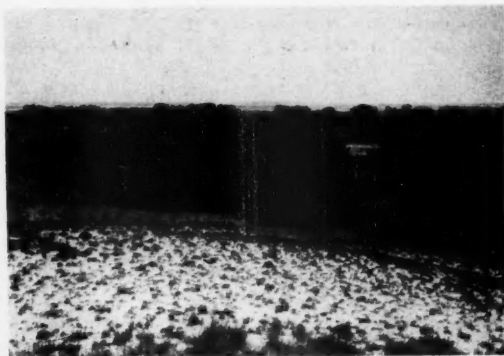


FIG. 6. Trees along the Saline River northwest of Hays, Kansas. The chief species are hackberry, American elm, green ash, and cottonwood (*Populus sargentii*).

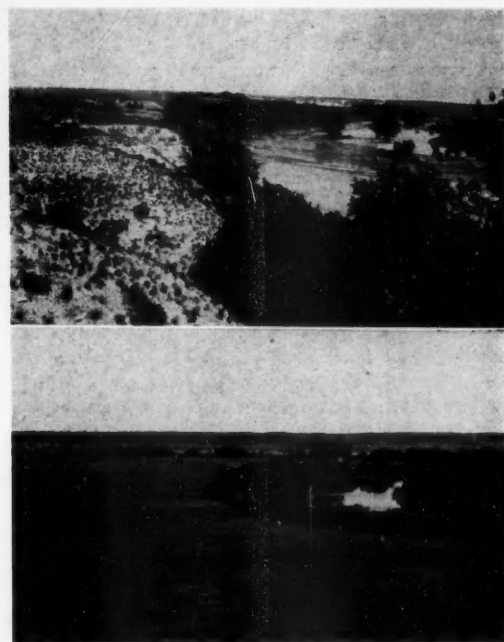


FIG. 7. (UPPER) Trees growing in the protection of a north-facing slope along the Saline River 16 miles northwest of Hays, August, 1941. (LOWER) View along the James River in eastern South Dakota showing the absence of trees except on the river banks.

some of the most protected sites and often occur as individuals rather than in groups (Fig. 7).

A comparison of the forest communities and their structure in the eastern portion of the prairie climax with that of distribution of trees farther westward reveals striking differences. Distinct communities along the Missouri River in southeastern Nebraska, for example, extend westward for short distances over the uplands, but farther along the major streams.

An associates dominated by ash, elm, and cottonwood is typical of the flood plains. In fact, communities representing different stages in its development may be seen. Various willows, cottonwood, and boxelder represent an early stage, with sycamore (*Platanus occidentalis*) in local areas. Species of elm and ash, hackberry (*Celtis occidentalis*), and black walnut form a later one. Other common trees on well-developed flood plains are Kentucky coffeetree (*Gymnocladus dioica*), black cherry (*Prunus serotina*), and much less frequently buckeye (*Aesculus glabra*).

Red oak and linden constitute the most mesic community; a rather constant component is the understory of ironwood (*Ostrya virginiana*). Here also are found black oak (*Quercus velutina*), yellow oak (*Q. muhlenbergi*), bur oak, shagbark hickory (*Carya ovata*), bitternut hickory, red and white elm, redbud (*Cercis canadensis*), and occasionally trees of several other species. Black oak and shagbark hickory form distinct though small communities in less mesic sites, often on upper slopes of hillsides above the community of red oak and linden.

The most xerophytic associates and consequently that of greatest extent is bur oak-bitternut hickory. The bur oak, which is by far the most important species, extends westward along the streams more than half way across Kansas and Nebraska, but to the Black Hills in the northwest. A score of other species of trees are found in these forests near the Missouri River, including some of all of the upland species previously mentioned but also red mulberry (*Morus rubra*), prairie crabapple (*Malus ioensis*), red cedar (*Juniperus virginiana*), hawthorn (*Crataegus mollis*), and honey locust. These, of course, may sometimes occur in the other communities as well.

Shrubs form a layer in these forests, the density of which varies with the amount of light reaching them through the canopy of trees. Where this is closed and dense many intolerant species fail to survive. Thus, in the deep shade of the red oak and linden forest there is no distinct layer of shrubs but only an occasional plant of prickly ash (*Zanthoxylum americanum*), wild black raspberry (*Rubus occidentalis*), or the twining honeysuckle (*Lonicera dioica*), and the climbing Virginia creeper (*Parthenocissus quinquefolia*). Mesic species of infrequent occurrence in these forest outposts are pawpaw (*Asimina triloba*) and redbud.

In the bur oak forest, especially, shrubs are abundant (Fig. 8). Here are found hazelnut (*Corylus americana*), prickly ash, buckthorn (*Rhamnus lanceolata*), raspberries (*Rubus strigosus* and *R. occidentalis*), dogwoods (*Cornus asperifolia* and *C. amomum*), and burning bush (*Euonymus atropurpureus*). Virginia creeper, wild grape (*Vitis vulpina*), bitter-sweet (*Celastrus scandens*), and poison ivy (*Toxicodendron radicans*) are the chief climbing vines. Gooseberry (*Ribes missouriense*), coralberry (*Symphoricarpos orbiculatus*), and the western snowberry (*S. occidentalis*), wild plum (*Prunus americana*), and smooth sumac (*Rhus glabra*) are very common.



FIG. 8. Young oak-hickory forest on a hilltop in eastern Nebraska. Note the abundance of shrubs.

These shrubs extend outward to a considerable distance from the forest margins and the more xeric ones are found commonly even along small streams or in pockets in ravines. The wild plum forms thickets far from the woodland, smooth sumac behaves in a similar manner, and the species of *Symphoricarpos* are to be found where trees fail to grow.

The transition from these forests, with their layers of shrubs and woodland herbs and ground layer of mosses, lichens, and fungi, to the remnant of trees which occur farther westward is rather rapid. Most species soon reach their limits of tolerance to aridity, forest structure and community groupings gradually disappear, and size, rate of growth, and longevity of individuals all decrease as the environment becomes more and more unfavorable for trees. Finally they are found, if at all, only in small groups or as scattered individuals. Since the effects of drought on growth were studied most intensively in the western half of Kansas, distribution of the trees there will be described. Conditions there, however, are typically representative of the distribution of trees over vast areas of the dry mixed prairie, as those just described are in general representative of conditions of forests in the less arid true prairie eastward.

Native trees in western Kansas are mostly limited to banks of the larger streams and to broad, shallow ravines that are tributary to them (Fig. 9). They are mostly cottonwood and are widely spaced in the beds of moist intermittent streams. Scarcely any shrubs

occur. Instead the soil beneath the trees is often occupied by grasses, mostly sand dropseed (*Sporobolus cryptandrus*), blue grama (*Bouteloua gracilis*), or buffalo grass (*Buchloe dactyloides*). Where grasses were few or absent, sunflowers (*Helianthus annuus*), lamb's quarters (*Chenopodium* spp.), Russian thistle (*Salsola pestifer*), and other weeds often formed the lower story of vegetation. Usually no ponds from runoff water occurred, hence little storage of water resulted from dashing rains. Thus, sites favorable to the growth of trees were few.



FIG. 9. (UPPER) American elm and cottonwood in a broad, shallow ravine in a range 5 miles west of Phillipsburg, Kansas. (LOWER) Cottonwoods sparsely spaced in a shallow ravine north of Syracuse, Kansas, near the Kansas-Colorado state line. August, 1943.

Along sandy streams and rivers, as the Smoky Hill and Arkansas, woody plants are usually limited to a few species of trees and shrubs which grow in open stands. The trees, mostly cottonwood and willow, are usually restricted to small sandbars in the river bed, or to large bends where the stream flow is considerably retarded in times of high water (Fig. 10). Small clumps of shrubs, especially indigobush (*Amorpha fruticosa*) and sandbar willow (*Salix interior*), are common but never abundant.

Streams that flowed continuously through areas of loam soil ("hard lands") maintained a supply of water for plant life; here the stands of trees and shrubs were not so sparse (Fig. 11). Even where the trees were located 8 to 12 feet above the water surface of the stream, their roots penetrated to the water table and were thereby able to secure enough moisture to survive even the most severe drought. Along such streams, trees and shrubs were found bordering both banks. Where a steep bank formed a

north-facing slope the environment was even more mesic, as was indicated by the close cover of trees and shrubs. On the south-facing slopes the trees were fewer. Woody vegetation on the gentle slopes of the flood plains was usually limited to an open stand of trees and occasional clumps of the more xeric shrubs. The trees were frequently about equally divided in number among hackberry, American elm, and green ash. Also scattered sparsely among these were boxelder and cottonwood.

An understory of woody vegetation, composed mostly of coralberry, occurred on the gentle slopes. Wild grape, poison ivy, indigobush, and smooth sumac were common on steep north exposures. In fact, the shrubs often formed a fringe above the zone of trees near the upper part of the slopes. Farther upstream, which was also usually farther westward, the flow of water was intermittent and the stand of trees was distinctly more sparse. Here the cottonwoods formed a narrow, broken belt on each side of the stream. Occasional clumps of indigobush and wild plum also grew near the trees. Often no



FIG. 10. Cottonwoods and willows along the sandy Smoky Hill River near Hays, Kansas. They are most abundant in the bends of the river where small flood plains have been built up. August, 1941.



FIG. 11. Trees confined to lower banks along Big Creek near Hays. Photo in late autumn.

trees occurred for long distances; the soil was clothed with tall grasses and weeds.

Springs that continued to flow throughout the drought supplied enough water in some places to form permanent ponds. Around these grew a luxuriant cover of woody vegetation (Fig. 12). The most abundant trees were cottonwood and willow. Shrubs were numerous. Those most common were the sandbar willow, indigobush, and snowberry.



FIG. 12. Willows (foreground) and cottonwoods in a marsh fed by continuously flowing springs near Hays. All the trees are alive. October, 1939.

Many of the streams of western Kansas had only an intermittent surface flow during the drought. Some of these ran through a sandy loam soil usually underlain with strata of shales. The population of trees and shrubs along them became quite sparse since many of the roots were above the lowered water table. Their distribution was limited to occasional clumps in the most favored locations. Sometimes, however, moderately dense stands of trees extended for considerable distances, especially along north-facing slopes.

Trees and shrubs occurred at some distance from the stream bed where there were steep protecting slopes. On steep north-facing slopes with a mantle



FIG. 13. Native red cedars (*Juniperus virginiana*) growing on a limestone escarpment along Big Creek, 20 miles southeast of Hays. The deciduous trees along the stream have only sparse foliage, so severe was the drought. October, 1939.

of soil at their bases, trees frequently grew in abundance. In such sites red cedar often formed an important component of the woody vegetation (Fig. 13). The deciduous trees were usually American elm, hackberry, green ash, and boxelder.

In the heads of ravines often several miles from the streams conditions were quite xeric. But clumps of dwarfed hackberry and American elm were frequently found on the north-facing slopes (Fig. 14).



FIG. 14. Thin stand of dwarfed hackberry and American elm in a dry ravine near Hays. The sparse foliage is a result of the drought. October, 1939.

On the barren south-facing ones there was seldom more than an occasional small tree or clump of shrubs such as ill-scented sumac (*Rhus trilobata*), New Jersey tea (*Ceanothus ovatus*), or smooth sumac (Fig. 15).

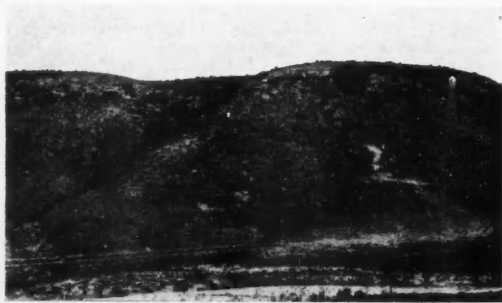


FIG. 15. Scattered plants of ill-scented sumac (*Rhus trilobata*) on a steep south-facing slope. Runoff was sufficient to remove nearly all the soil, leaving the underlying limestone exposed. October, 1939.

Where wide, shallow ravines extended to considerable distances from the main stream, water seldom flowed except for a brief period while carrying away the runoff from rains that fell on the adjacent watersheds. Here trees grew in clumps or were scattered thinly along the center of the ravines where their roots penetrated far into the black alluvial soil (Fig. 16). Hackberry, American elm, and ash were most

commonly found with occasional occurrence of coral-berry and snowberry on the gentle slopes. The steep north-facing slopes were often populated with a thin stand of ill-scented sumac, smooth sumac, and wild grape.



FIG. 16. Green ash, hackberry, and American elm in a broad, shallow ravine north of Stockton, Kansas. June, 1944.

VALUES OF TREES IN PRAIRIE

The greatest value of trees in prairie does not lie in financial returns from the utilization of the timber. Protection against the cold winds and drifting snow of winter and the hot drying winds during summer are of great importance to the welfare of the dwellers in the prairie. As stated by Shelford (1944): "After the eastern part of our continent had been occupied, there was a gradual shifting westward into the parkland areas which were characterized by groves of trees and trees along streams. There were rather large stretches of prairie between them in Illinois, and still larger stretches in Iowa and eastern Nebraska. The early settler avoided the prairies; at first in part for the reason that he thought they were not fertile because they were treeless. As his experience increased, there were added to this reason the menace of the prairie fires and the terror of winter storms."

Wood for the construction of buildings, for fences and for fuel, indispensable to the early settler, was to be found only along the streams. This scarcity of fuel was attested by the use of "cow chips," and the sturdy Kansas pioneer frequently obtained posts for fences by quarrying the rock from distant hillsides (Fig. 17). Also timber meant the proximity of water, and although permanent streams and continuously flowing springs were much more abundant than they are today, yet the problem of an adequate supply of water was an ever present one, at least farther westward. As settlements extended into the prairies, the pioneers soon planned to surround their homes with trees. This was encouraged by the Timber Culture Act of 1873. It resulted in the planting of many thousands of acres of trees in prairie, since a timber claim provided free title to an additional quarter section of land. Despite the fact that, for many reasons, most of this planting was futile, frequently such plantings did survive. Also thousands

of groves were planted and nurtured by settlers bound by no legal obligations. They were planted solely because these homemakers appreciated the value of trees. Some of these planted groves still remain as living witnesses of the initiative and foresight of the prairie pioneers.



FIG. 17. Natural reproduction of red cedar along a fence in prairie where the seeds have been carried by birds. The post was hewn from the native rock.

The value of belts of trees in protecting crops from damage by desiccating winds is well known; such protection may result in increase in yields and at times avert crop failure. Protection of dwellings, farm buildings, and stock from wind and sun by suitably located trees adds immeasurably to the comfort of both man and his domestic animals. Protection to vegetable gardens, flower gardens, and orchards was afforded by trees, and in groups they were also very effective in preventing soil erosion. Many species of birds seek the shelter of trees and groves; they may forage widely for food and destroy many harmful insects, but return to trees for shelter, to build their nests and rear their young. Such shelter from the elements and their natural enemies is sometimes pitifully scarce. In remnants of a timber claim near Burlington, Colorado, flocks of mourning doves had nests at the rate of 6 to 8 per tree, some only a few feet above the ground (Fig. 18). Quail are usually found only where trees or shrubs are present in sufficient numbers to provide them protection and a home. Even such grassland birds as grouse and pheasants prefer the protection afforded by trees and shrubs to that of the herbaceous growth of the drier prairies. Other animals generally abundant eastward are in prairie found only where there is timber, particularly along the streams.

To the dweller of forests, the prairie pioneer, the landscape of the treeless grassland seemed extremely monotonous. There was an innate longing for the companionship of trees. His immediate ancestors were from the eastern deciduous forest, and theirs were from the forested continent of Europe. Man has always looked with awe and reverence upon a tree. It represents permanence—long periods of life, often the growth of centuries. Forest groves were man's first temples and were early used for religious rites



FIG. 18. Remains of a timber claim near Burlington, Colorado, in 1924. These ash trees are 37 years old, but only 3 to 4 inches in diameter and about 18 feet high. Note invasion of grasses, chiefly sand dropseed (*Sporobolus cryptandrus*), in the foreground.

and ceremonies of various primitive peoples. Trees have always been a part of man's aesthetic and social life. The prairie pioneers used groves along the streams for places of recreation. Here the cool damp shade was indeed a welcome contrast to the sun and heat of the grassland. Pienies, religious gatherings, and political conventions were held under the protection of a dense growth of cottonwoods or the spreading canopy of the American elm. The recreational, aesthetic, and social values associated with groves and shade trees, though intangible, are nonetheless of high importance in the life of the individual. Trees lend a homelike and sheltered aspect. They beautify the environment and add to the happiness of man. A tree in a prairie landscape is a landmark in the distance, its growth is a measure of time, it is a part of the life of the community which everyone shares.

EARLY EFFECTS OF DROUGHT

The early effects of drought were so impressive and so widespread that numerous reports and statements are to be had. A summary of these early losses constitute therefore a more or less comprehensive review of the literature.

OBSERVATIONS IN 1934

Behavior of trees and shrubs during the severe drought in 1934 was studied along the valleys near Weeping Water in eastern Nebraska, where the prairie meets postclimax forest. Observations late in July showed that the leaves of smooth sumac had been wilting for many days. Rough-leaved dogwood (*Cornus asperifolia*) was also very much wilted, often beyond recovery. Many bushes of Missouri gooseberry were clothed with dead, yellow leaves, and the wild grape had grown into the sunlight only to have its foliage burned in the withering heat. Often the entire tops of black raspberry were dead. Beneath the shrubs were found groups of white avens (*Geum canadense*), Solomon's seal (*Polygonatum biflorum*), and other woodland herbs withered and often bleached white. The common chokecherry (*Prunus virginiana*)

and sandbar willow (*Salix interior*) were frequently nearly defoliated and the tops of peach-leaved willow were often dry. The larger and better rooted older trees of these marginal forests were least affected.

The marginal postclimax forest at Weeping Water likewise bore the marks of severe drought. The water in the stream was very low and Cascade Creek, its main tributary, was dry. Even at a distance considerable damage could be detected among the crowns of the trees and closer examination showed that many individuals of most species had been injured.

On the flood plain the leaves of boxelder were wilted and dried, sometimes on the upper half or the unshaded portions of the trees only but often throughout their entirety. Various tree willows had suffered a similar fate (Fig. 19). Where soft maple occurred, nearly all the leaves were dried and discolored as by frost; similar injury was found in whole groves planted on uplands. The crowns of green ash were half dried and brown as a result of the scorching heat. Many trees of both American elm and red elm had wilted crowns. The scorched leaves did not turn brown or bleach white as did those of other species, but took on a bluish-gray color and soon fell to the ground. Black walnut was scarcely affected, perhaps as a result of its excellent root system, nor were trees of this species injured in even drier sites. Hackberry appeared to be in fair condition. Missouri gooseberry, elder (*Sambucus canadensis*), and species of *Symphoricarpos*, all of the flood plains, were badly scorched, especially where they were exposed to direct insolation by clearing. Wild grape, poison ivy, and greenbrier (*Smilax hispida*) showed many dead or half-browned leaves. Under the trees many herbs, especially the wood nettle (*Urticastrum divaricatum*) and pale touch-me-not (*Impatiens pallida*), appeared as if seared by a surface fire; sometimes a few uppermost green leaves persisted.

In the bordering belts of linden and red oak on steep north-facing slopes, one-third to one-half of the leaves of the shallowly rooted linden were brownish yellow and functionless; many had fallen to the ground (Fig. 20). The more deeply rooted red oak had shown as yet no permanent injury although the portions of the crown most exposed to the sun were wilted even in early morning. The severity of the drought was attested by the behavior of poison ivy. Long established vines, two inches in diameter, bore wilted leaves even in the shade in early morning, from the crown to the base of the tree. Virginia creeper had many leaves destroyed by drought. Where these lianas formed a ground layer, more dead than living foliage occurred. Wild grape often bore abundant ripening fruit, but the leaves were dead. Smooth-leaved honeysuckle and bittersweet were wilted. The mesic bladdernut (*Staphylea trifolia*) had both wilted and dead foliage. The black raspberry was killed back from the tips. The usual, rich ground layer of herbs was sadly depleted by the drought.

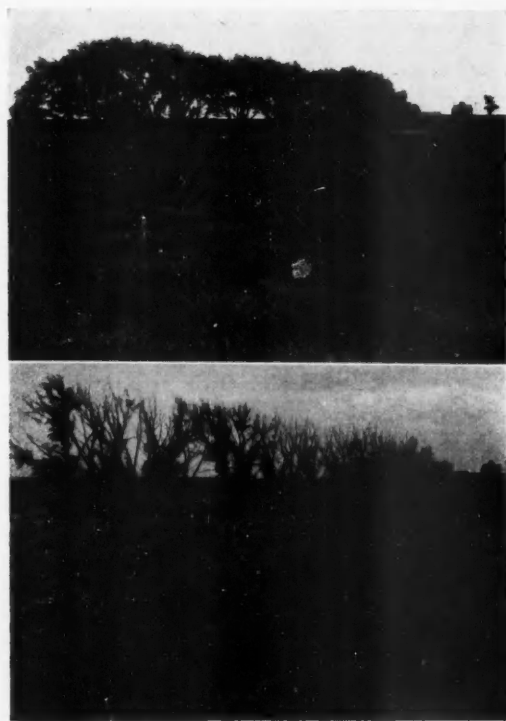


FIG. 19. (UPPER) Peach-leaved willows (*Salix amygdaloides*) on low ground with high water table near Lincoln, Nebraska. Note bluegrass (*Poa pratensis*) pasture in foreground. June, 1933. (LOWER) Same view showing death of willows and bluegrass by drought and replacement of bluegrass by rough pigweed (*Amaranthus retroflexus*) and other weeds. June, 1935.

Missouri gooseberry was half dead in the deep shade of this mesic forest type; rough-leaved dogwood was often wilted or the leaves dried; coralberry showed occasional injury. On the scattered growth of hazelnut the leaves were completely killed. The foliage of the rather dense layer of ironwood showed great drought injury both to seedlings and to well established trees. Sometimes the seedlings of the red oak and more often those of the linden were parched and burned.

In the bur oak forest that covered the upper slopes of the hills, often alternating with shrubs or grassland on the wind-swept tops, even greater drought prevailed. From a vantage point on a ridge, one could clearly see that many of the tops of the bur oaks had been badly scorched and that the leaves were dried. Often isolated trees or small groups withstood the drought best, partly because of their better developed root systems and especially because of the better circulation of the air about them, which reduced the high temperatures caused by the intense insolation. Where small openings occurred in the forest but general wind movement was retarded,



FIG. 20. Forest of red oak and linden on rocky north-facing slope on Cascade Creek near Weeping Water, Nebraska. Photo in spring before the drought.

seald injury to the bur oak often extended to the lowest branches. Scattered trees of wild black cherry with nearly all of the leaves burned were common. Elms were wilted or half defoliated in the oak forest. Intermixed trees of green ash, linden, ironwood, hawthorn, and other species were badly burned. The damage to red oak was less marked. In general it was in the tops of the crowns, which were under full insolation, that injury was most severe. Oak seedlings less than two feet tall were often damaged by the drought, but those more firmly rooted grew unharmed. Where seedlings two or more years old had invaded the adjoining grassland and made contacts with the soil below the roots of the grasses, they stood out prominently above the drying or dead blue-stems and remained green until late fall.

The effect of heat was also often noted on the individual leaves. Where the cupped, drooping leaflets of sumac hung from the great horizontal midrib, for example, it was not the shaded tips that burned, despite their less advantageous relation to the water supply, but the arched bases which received the full impact of the sun. Thus, the basal half of the leaf was dead and the distal half still green.

The scattered undergrowth of Missouri gooseberry, prickly ash, and hazelnut on higher ground was as dry and brown as if subjected to heavy frost. In less xeric situations a few green leaves remained on the hazelnut, but everywhere they were at least half

dried. In their contact with the dried bluestems of the native prairie, the new growth was only one-fourth or less of that indicated by the dead, fire-killed stems of the preceding year, and even this scanty foliage was as dry and crisp as that of the prairie grasses. Smooth sumac and coralberry had suffered much, but less than their more mesic chaparral co-dominants. Drought clearly revealed the relative mesic or xeric tendencies of the several species of shrubs. Frequently the green tops of sumac extended above the burned leaves in a hazelnut thicket, or the green foliage of coralberry contrasted with the withered leaves of rough-leaved dogwood or the dead ones of prickly ash. Of the main dominants the sequence as revealed by drought confirmed that of distribution, namely, sumac in the driest places as well as farthest from the forest borders, coralberry ranking second, followed by the rough-leaved dogwood. The more mesic hazelnut, which outshades them all, withstands less drought and pioneers closer to the forest border. Prickly ash succumbed to drought first of all.

By the end of August the effects of drought were even more severe in the Weeping Water forest. Many half-grown trees of boxelder were dead and all the leaves on older trees had dried. Drying of the crowns of green ash had progressed, and many trees of red elm and white elm were half defoliated. Neither black walnut nor hackberry showed much injury. Missouri gooseberry, coralberry, and snowberry were practically defoliated; many stems of the coralberry were dead. Both leaves and stems of elder had died. Wilted poison ivy still persisted. Herbaceous vegetation had practically disappeared and the ground was partially covered with leaves as after an early frost.

Although linden showed no increased injury, the fruits had dried without maturing. In the crowns of red oak growing on midslopes most of the leaves were half dried and on many trees they were entirely dry. Accompanying bur oak showed little or no drought injury nor did the red oak on lower slopes. Ironwood showed much more drying than formerly; it was not confined to the high crowns but occurred on all of the branches including those of saplings. This species looked as though it had been seared by the heat of a ground fire. On higher slopes especially, the dead stems were abundant. The ground was strewn with the dried leaves of this understory species and those of the two dominants. The undershrubs all showed severe wilting and many had succumbed. The dead, dried stems of hazelnut were easily broken. Losses of tree seedlings had increased.

Many trees of red oak on the hilltops and upper slopes were defoliated; some had died. On lower southwest slopes the foliage of the upper half of the trees was so badly burned that nearly all of the leaves were withered. Everywhere the foliage of the undergrowth of Missouri gooseberry and ironwood was completely dried and many plants were dead. Other shrubs, such as coralberry, snowberry, and smooth sumac, and most lianas had suffered a similar

fate. Practically all herbaceous undergrowth had dried. But in pastures where competition was with bluegrass rather than bur oak, the coralberry, sumac, and hazelnut were still in fairly good condition.

Examination of the increment of wood laid down in the annual ring of 1934 showed that it was very narrow even in trees on the flood plain. It seldom exceeded one-third the width of that of 1933 and was sometimes only one-sixth as great.

Conditions similar to those at Weeping Water prevailed over much of eastern Nebraska and extended into the marginal forests of Iowa. Injury to shagbark hickory and various other trees was considerable. Westward the severity of drought increased. Woodlands bordering streams and planted groves in the western portion of the true prairie suffered the loss of many trees. Sometimes whole groves appeared dead, but the extent of the losses could not be accurately estimated until the end of another growing season (Fig. 21). Records of this terrible year of drought, the whole drought period, and the good years which followed, are to be found in the living survivors (Fig. 22).



FIG. 21. Drought-damaged trees of northern catalpa (*Catalpa speciosa*) bordering the west side of a large old grove of silver maple (*Acer saccharinum*). The maples were all killed by the drought and removed for firewood. The few surviving trees are about 50 years old and 33 feet high. Photo near Elmwood in eastern Nebraska, September, 1943.

STUDIES IN THE NORTHERN PRAIRIES

As a result of the severe drought and hot winds which occurred during 1934 in western Minnesota, following a number of dry years, heavy damage occurred to shelter belts (Deters and Schmitz 1936). Losses had been heavy since 1932, but in 1934, in certain parts of the prairie region, it seemed that only a comparatively small number of plantations would survive. Five species, boxelder, willow, green ash, silver maple, and cottonwood (in order of their abundance), composed 90 percent of all the 28 species occurring in the shelterbelts. These also occurred commonly in or adjacent to the prairie region. A

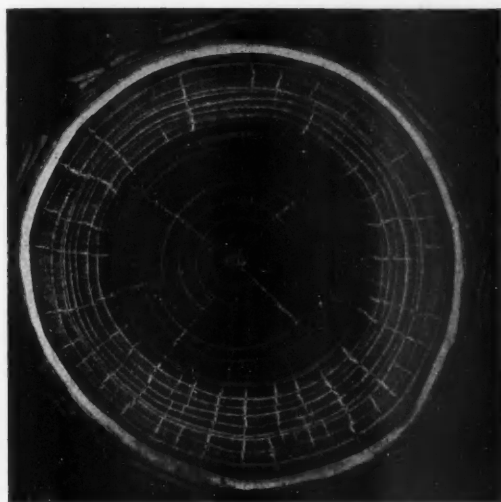


FIG. 22. Section of red elm growing on the south-facing slope of a rocky hillside near Weeping Water. The very narrow ring near the edge of the dark wood was put down during the extremely dry year, 1934. The next year was one of good rainfall as were also the years 1941 to 1943.

very extensive survey in 11 counties revealed that 25.5 percent of all the 28 species of trees examined were dead and that 14.5 percent had dead tops. Thus, 40 percent of all the trees were considered dead or dying at the end of the summer of 1934. Of the five chief species cottonwood suffered most (48 percent) and green ash least (8 percent).

Effects of the drought in North Dakota have been summarized for the writers by the Extension Forester, Mr. J. J. Zaylskie and Dr. C. B. Waldron from their field observations since 1936. "Practically all cottonwoods 30 years of age or older were killed during the drought, except in those places where there was a high water table. This is true also of boxelder; only in this case the trees died back to the ground and put forth sprouts, forming a rather dense hedge or undergrowth. Because of this new growth of the boxelder many persons have a decided liking for it. Willow has probably suffered greater losses even than the cottonwood, and can now be found only in those areas adjacent to streams, or where the water tables have been 3 to 5 feet underground. Many of the old windbreaks of cottonwood, willow, and some of boxelder have been almost entirely killed and now appear as white ghosts against the sky line. Much of these windbreaks was salvaged for fuel, posts, or rough timber. Still many millions of feet of rough lumber remains standing; but in most cases where the trees were not killed outright they have stagnated, the tops dying while the lower portions have straggly growths. Windbreaks and tree plantings in the Red River Valley did not suffer so severely during the drought years; but most plantings west of the valley were

greatly damaged. In some counties at least 50 percent of the trees were killed during the period 1934-1936."

Ellison and Woolfolk (1937) state that the widespread drought of 1934 was the most severe in the recorded history of southeastern Montana. "In the summer of 1935 [near Miles City], yellowing foliage and dead individuals in many stands of pine and juniper attested the severity of the drought on upland trees, and 1934 diameter increments were, in the main, less than those of other years. In many stream bottoms tracts of cottonwoods had been injured and even killed. The heaviest losses of trees were on high ground where the original stand of trees and undershrubs was only half as dense as near the river. Previous dry years, especially 1931, have probably contributed to the damage." Much injury to woody plants was observed in stands of pine, juniper, cottonwood, sagebrush, and other species.

STUDIES IN THE CENTRAL PRAIRIES

Ramsey (1936) in discussing drought susceptibility of evergreens in Iowa, states that the history of windbreaks in that state began with the planting of quick-growing species of trees—cottonwoods, willows, boxelders, and silver maples—when the open prairie began to be dotted with farmsteads (Fig. 23). Since these short-lived deciduous trees failed to give adequate protection against winter winds, the farmers turned their attention to evergreen windbreaks. These were desired about farmsteads because of their ability to effectively check winter winds, and because they do not require so large an area as deciduous trees. Cooperative, experimental plantings of windbreaks were made in 1922. "Early in the spring of 1934 many observations of winter injury to evergreens were made, and reports came from all parts of the state of severe losses of both small and large trees." It was considered that evergreens are most subject to drought injury in winter. Losses by death were between 5 and 9 percent for ponderosa pine, white cedar, and Norway spruce, 10 percent for white pine,



FIG. 23. Cottonwood trees 2 to 2.5 feet in diameter in a pasture near Anita, Iowa. They died early in the drought. May, 1939.

20 for Scotch pine, and 39 percent for red pine. Red pine, Scotch pine, white pine, and white cedar showed percentage of drought damage of 6, 10, 15, and 29, respectively.

That the series of hot, dry seasons since 1930 has taken a heavy toll of both planted and natural timber in Kansas has been pointed out by Ware and Smith (1939). While in eastern Kansas only 5 percent of planted forest trees on farms were dead or had dead tops in 1936, in the central part 18 percent death and 23 percent injury was recorded. Trees in the western third of the state had suffered even more. Thirty-five percent had died and 20 percent had dead branches in their tops early in the drought. Examination of large numbers of planted trees on farms and rural school grounds throughout the state gave the following losses in percentages based on trees standing in 1936, not on the total number planted: red cedar and bur oak 1, Osage orange 8, American elm 10, black walnut 18, cottonwood 21, catalpa 25, hackberry 35, boxelder and black locust 36, mulberry 38, silver maple 46, green ash 53, and honey locust 54.

A survey of all the trees on 253 acres in Manhattan, Kansas, during the summer of 1934, showed that 20 percent were dead or dying, and an additional 30 percent were definitely injured as a result of the drought and heat. In the parts of the city containing natural or wild areas, 24 percent of the trees were dead or nearly dead, and only 47.5 percent were apparently still sound (Stiles and Melchers 1935).

In northwestern Nebraska, trees, shrubs, and a rélict herbaceous flora meet in postclimax communities in the river valleys. Tolstead (1942) pointed out that "the deciduous trees [principally American elm, green ash, red ash, boxelder, hackberry, and cottonwood] grow in well aerated soils where moisture is available from a stable water table throughout the year (Fig. 24). Woodlands are common in the deep canyons and immediately along the streams, but the broad river valleys are usually occupied by scattered groves of trees alternating with chaparral and tall-grass meadow. The ecotone between the deciduous woods and the mixed prairie on the hillsides is narrow because of marked changes in depths to the water table. . . . Ponderosa pines grow . . . on rough stony land where run-in water is received from rock surfaces and where snow lodges during the winter. They are located well above the water table and must withstand varying periods of drought. Seedlings do not become established on broad, gentle slopes because the grasses are better equipped to obtain the available moisture. . . . Because deciduous trees are able to grow only where their roots have access to a permanent water table, there was little loss from drought. Ponderosa pine is especially resistant to drought, and only rarely were trees killed. But in a few dry canyons, which did not have a favorable water supply, mortality of the chaparral was as great as 85 to 95 percent."



FIG. 24. View from Chadron State Park in northwestern Nebraska, showing ponderosa pine (*Pinus ponderosa*) growing on the stony uplands and deciduous trees in the valley where there is a stable water table throughout the year. Photo by W. L. Tolstead in 1940.

STUDIES IN OKLAHOMA

Working in central Oklahoma, Harper (1940) states that severe drought during the years 1932-40 destroyed 20 to 50 percent of the trees in some areas of shallow upland soils where a xerophytic type of forest was growing or on bottomland soils containing a high percentage of clay where a mesophytic type of trees had developed.

Survival of trees that were alive at the beginning of drought in old shelterbelts in territory surrounding Goodwell, Oklahoma, was reported in 1938 by Bunker and Thomson. In order to obtain data in all habitats in which trees must live in that area, studies were made of shelterbelts on both shallow and deep soils, in cultivated and uncultivated areas, and in both moist and dry sites. By 1937 losses of red cedar were only 13 percent and those of Osage orange 35 percent. Honey locust lost 55 percent, ash 75, and black walnut 79 percent even this early in the drought. Only older, well established trees were studied, but trees in this region are very short-lived and at the age of 30 years appear to be mature.

LOSSES IN GENERAL

A rapid reconnaissance of tree plantations in a wide territory within which the shelterbelt zone was to be marked out, was conducted by Kaylor, Starring, and Ditman (1935) in the autumn of 1934. The percentage survival of trees, where survival is the proportion of living trees to the total number of trees found in the groves when examined and not the number originally planted, is shown in Table 1. These surveys were made in a strip 2 miles wide and extended from east to west almost across Kansas and Nebraska except for the width of two or three of the most easterly counties. In the Dakotas they began at the eastern boundary but did not extend so far westward; the southern strip extended westward from central Oklahoma into the panhandle of Texas. Results are shown in Table 1.

TABLE 1. Average survival of principal species examined in plantings.

Species	Groves in which occurring	AVERAGE SURVIVAL		
		In groves under 30 years old	In groves over 30 years old	In all groves
	Number	Percent	Percent	Percent
Green ash.....	635	48.5	20.4	29.5
Cottonwood.....	459	34.0	24.5	27.1
Boxelder.....	456	36.1	20.2	25.2
Mulberry.....	403	25.6	12.9	17.4
American elm.....	223	38.0	20.1	30.2
Black locust.....	208	20.8	23.3	21.9
Catalpa.....	127	26.6	9.7	20.1
Eastern red cedar	93	94.9	92.4	93.2

Survival by states was: North Dakota 43.1 percent, South Dakota 31.8, Nebraska 17.8, Oklahoma-Texas 28.4. Data for Kansas were not given. They found:

"The average heights of trees over 30 years in age of certain key species—those which usually give character to the groves—are as follows: cottonwood, 50 feet; American elm, 27 feet; green ash, 26 feet; black locust, 26 feet; and eastern red cedar, 17 feet. These values represent a general average for the region.

"Drought is undoubtedly of primary importance as a factor of damage and also as a test of the ability of individual species planted in shelterbelts to survive. During and after 1931, moisture conditions for plant life in the prairie-plains region became increasingly acute, and the summer of 1934 provided a devastating climax to the dry period.

"Although considerable losses had been reported before 1931, the majority of the shelterbelts seemed to have held their own fairly well despite moisture shortage, sleet, rodents, grazing, and insects. But the parching winds and searing temperatures of the last three years proved to be more than many of the trees could withstand" (Fig. 25).

THE CHANGING ENVIRONMENT

The prairie environment varies from semihumid near the deciduous forest to semiarid in the west. The region under consideration (from central Iowa westward) is, in general, characterized by relatively low annual precipitation occurring mostly during summer, frequent droughts (especially westward from the Iowa-Nebraska state line), and great range in extremes of temperature. Humidity is relatively low, and much wind, sometimes hot and desiccating and often of comparatively high velocities, occurs. Winds blow with considerable regularity over the level or undulating prairie landscape, and rate of evaporation is high in comparison with the amount of precipitation.

PRECIPITATION

Low precipitation in the Midwest is serious for trees not only because of the relatively small amounts but especially because of its erratic distribution. This applies not only to dry cycles but also to periods of drought during years of normal precipitation. More-

over, rainfall, especially in mixed prairie, is usually followed by clear, hot days and high wind movement, both of which promote rapid drying of the soil and high rates of transpiration.

A comparison of the distribution of the mean annual precipitation in true and mixed prairie before the great drought is pertinent to an understanding of the decreased natural distribution of trees west-



FIG. 25. (UPPER) Tree claim 8 miles northwest of Hays. Many of the green ash and a few honey locust (*Gleditsia triacanthos*) are still alive, but the Osage orange (*Maclura pomifera*) and American elm are nearly all dead. September 19, 1939. (LOWER) Tree claim of Osage orange 4 miles southwest of Hays, October, 1939. All of the trees died early in the drought.

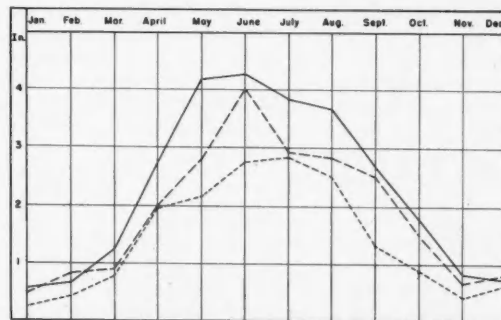


FIG. 26. Graphs showing the distribution of the mean annual precipitation in inches at Lincoln, Neb. (unbroken line), Phillipsburg, Kan. (long broken lines), and Burlington, Colo. (short broken lines).

ward. The data are from Lincoln in true prairie in eastern Nebraska, and from Phillipsburg (60 miles north of Hays) in mixed prairie in north central Kansas, and Burlington in eastern Colorado (Weaver 1924) (Fig. 26).

Casual examination of Figure 26 shows that most of the moisture falls during the growing season and only about one-tenth during the three winter months. Mean annual precipitation at the three stations from east to west is 28, 23, and 17 inches, respectively. The normal decrease of 5 inches at Phillipsburg from that at Lincoln, as well as the further decrease of 6 inches at Burlington, is quite evenly distributed throughout the year. The type of rainfall is quite similar throughout, consisting usually of heavy showers, often of short duration. This, however, is more marked in mixed prairie than in true prairie where the rains are more general. Westward, relatively more of the precipitation falls in light showers of 0.20 inch or less, which are of little or no value in increasing water content of soil.

Normal precipitation for the states of Kansas and Nebraska and the annual precipitation for the several years before, during, and after the drought are shown in Figure 27. The normal precipitation is that calculated for 1930; it is somewhat lower now because of the drought years. That the annual precipitation for Kansas was higher every year than that for Nebraska is due to two causes. Kansas extends somewhat farther east and not nearly so far westward as Nebraska, and precipitation here increases somewhat southward along a meridian. It may be noted that a period of dry years preceded the severe drought. Precipitation was lowest in 1934 and 1936, but because of previous desiccation of soil and vegetation 1939 was also one of the worst of the drought years. Any recovery of vegetation, herbaceous or arboreal, during 1935 and 1938—and there was considerable—was usually of little significance because of the following extremely dry years.

After the second year of extreme drought, the cover of grassland was greatly reduced and wind-blown dust effectively prevented rapid infiltration of water into the bared soil. Consequently, following showers much of the water rushed down the slopes into the streams where it was carried away rapidly (Fig. 28). Erratic distribution of precipitation, always a hindrance in this region to a continuous supply of available water, was very pronounced during the dry cycle. For example, in 1935 at Hays, Kansas, a rainy period of seven weeks duration in spring was followed by one of equal length during which there was scarcely any rainfall.

SOIL MOISTURE

Low available water content of soil occurs even during good years in true prairie. In mixed prairie water becomes nonavailable for plant growth at various depths during summer drought. The following conditions which prevailed in soils of silt loam texture during three years of almost normal precipitation are representative. Throughout the growing

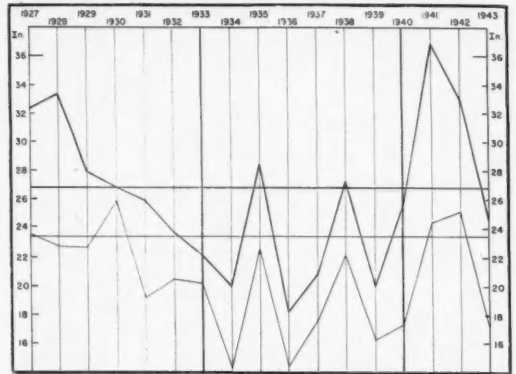


FIG. 27. Annual precipitation for Kansas (upper graph) from 1927 to 1943 inclusive, and normal precipitation (26.87 in.), heavy horizontal line. Annual precipitation for Nebraska (lower graph), and normal precipitation (23.50 in.), light horizontal line. The years of most severe drought lie between the heavy vertical lines.



FIG. 28. A stream near Hill City, Kansas, which formerly flowed continuously as a clear brook with many stretches where the water was held in deep pools. Since the occurrence of overgrazing, cultivation, and drought, torrents of water first washed the channel deep and then partially filled it with alluvial soil. The water table was lowered several feet and even during good years this stream is now only intermittent.

season of 1920 at Lincoln sufficient water was available at all depths to promote good growth. In the mixed prairie at Phillipsburg, July and early August were periods of soil drought and, at times, of actual deficiency of available water. At Burlington water content was favorable until June, but thereafter marked deficiencies were of frequent occurrence.

In 1921 an available supply of 5 percent moisture and usually 8 to 10 existed at all times and at all depths to 4 feet. At Phillipsburg water available for growth was almost exhausted once in July and twice in August; no water was available to a depth of 4 feet late in August. Conditions at Burlington were, as usual, much worse. At no time was water available in the third or fourth foot, while after June 30

it was depleted repeatedly in the first and second foot.

In 1922 at Lincoln, notwithstanding a late summer drought, a margin of at least 5 percent of available water was found at all depths of sampling. A period when little or no water was available in the prairie soil occurred at Phillipsburg in June, and this condition was nearly constant from the middle of July until autumn. Rather continuous soil drought prevailed at Burlington after the middle of June, broken only occasionally by available moisture in the surface soil.

A continuous weekly record of available water content of soil in upland prairie has been obtained since 1918 at Lincoln and since 1933 at Hays. Complete data during the growing season for the years just before, during, and following the drought have only recently been published (Albertson & Weaver 1942, Weaver & Albertson 1944). Hence, only a general summary of conditions need be given here. At Lincoln there was water available for growth at all depths to 4 feet in 1932 and nearly always 5 to 10 percent was available. Similar conditions prevailed in 1933, except that percentages of available moisture were less. Although there was a good supply of soil moisture in the spring of 1934 it was gradually depleted, and by July 30 no water to a depth of 4 feet was available for growth, and less than 2 percent to 6 feet depth. Very similar conditions prevailed through August, and only the surface foot of soil was moist until April of the next year. Available water in 1935 was moderate in amount, and low after midsummer, but no serious deficiency occurred. But in 1936 available water below 2 feet rarely exceeded 2 percent. Water in the first 2 feet became exhausted in June and remained un replenished until fall. In early fall no water was available at any depth to 5 feet. While there was 5 to 10 percent of water continuously available at 4 to 6 feet in 1937, the amount in the 2 to 4 foot depth was small, and at 1 to 2 feet usually less than 2 percent. No available water occurred in the surface foot late in August or early in September. The next year was one of abundant soil moisture at all depths to 6 feet, with only one dry period, in August. Dry periods, when the surface 6 inches of soil had no available water and the second 6 inches and the second foot had but little, occurred in May and August of 1939. During a very severe drought late in June and July of 1940, all available water was exhausted in the first and second foot and the amount in the deeper soil to 5 feet was reduced to less than 2 percent. But in 1941 to 1943, inclusive, water for plant growth was available at all times and at all depths to at least 6 feet, and it often occurred in large amounts.

At Hays there was about 2 percent residual water available to plants at certain depths below 2 feet in 1933, but none thereafter until 1941.² In the second foot of soil, water was nonavailable after the first

² Cracks and fissures, often concealed at the surface, frequently occurred in the thoroughly dried soils and permitted runoff water to enter and moisten the soil deeply in some places, but not generally.

week in June, 1933, and remained continuously unavailable except for two weeks in June, 1934, and during the entire month in 1935. From 1936 to 1940, inclusive, except for the last two weeks in July, 1940, the second foot of soil had no water available for plant growth. Even water in the surface foot was depleted to an amount nonavailable for growth during three two-week periods in 1933, one period of four weeks in 1934, and one seven-week interval in 1935. Three separate weeks without available water in 1937, two periods (one of five weeks and two of two weeks) in 1938, two periods each of two weeks duration and one in midsummer of four weeks, completed the record of the first foot until 1940. But even in that year of more than normal precipitation four separate weeks without available water in the surface soil occurred. Since nearly all these periods of deficient water in the surface foot occurred when water was also nonavailable at any depth to 5 feet, the prairie plants succumbed or became dormant. But the heavy precipitation in 1941 and especially in 1942 again wet the soil to a depth of at least 5 feet. In 1943 precipitation was low and the soil again became dry.

While these data are from upland soil covered, at least before drought, with prairie vegetation, they are probably fairly representative of conditions in old tree claims and windbreaks planted on similar upland soil. The supply of soil water on the hill-sides underlaid with limestone varied greatly. For example, repeated measurements of soil moisture in the first 24 inches above the limestone at Hays indicated that the supply became deficient late in June, 1933, and continued thus in the summer months during the worst years of drought. Samples of soil were also obtained from clay pockets and crevices running vertically through the limestone strata from 3 to 8 feet beneath the soil surface. The clay in these pockets had a high water content and the presence of myriads of roots indicated that during intense drought it was from here that much of the moisture was obtained.

LOWERING OF THE WATER TABLE

The low precipitation during drought did not recharge the ground water normally, and the adjustment of underflow together with discharge by transpiration, evaporation, and seepage to streams lowered the water table considerably in places (Condra 1944). The water table in many ravines and lowland terraces (first and second bottoms) fell 3 to 4 feet during the long period of drought (1933-1941) not only in Nebraska but also over much of the Midwest. In some instances it was even greater. With the lowering of the water table many streams stopped flowing. Lateral seepage often became less and the drying up of springs was common under the low rainfall. The movement of the water table beneath uplands, of course, is much slower and was measured only in tenths of inches. Where it is many feet below the soil surface it has no effect upon the growth of trees, since their roots extend downward only a relatively short distance.

TEMPERATURE

The high temperatures accompanying drought may be seen by an examination of Figure 29, where data from both Lincoln and Hays are shown. The year 1930 was selected as one with approximately normal predrought temperatures. Its temperatures are compared with those of the extremely dry year 1934. At Lincoln, increases above 1930 of 6° to 16.5° F. in mean temperatures were common until the middle of June, after which increases of 2° to 12° often occurred. During only three weeks were the mean temperatures lower than in 1930. Here also mean maximum temperatures were regularly 7° to 20.5° higher in early summer, and mean maximum temperatures of 101° to 107° occurred during three weeks in midsummer.

At Hays increases of 10° to 14° in mean weekly temperatures above those of 1930 were common until the middle of June, and 2° to 10.5° thereafter, except during three weeks when the mean temperatures were slightly lower than in 1930. The second week in July had a mean temperature of 92°. Except during four weeks, increases of 11° to 18° in mean maximum temperatures were common until late in July and

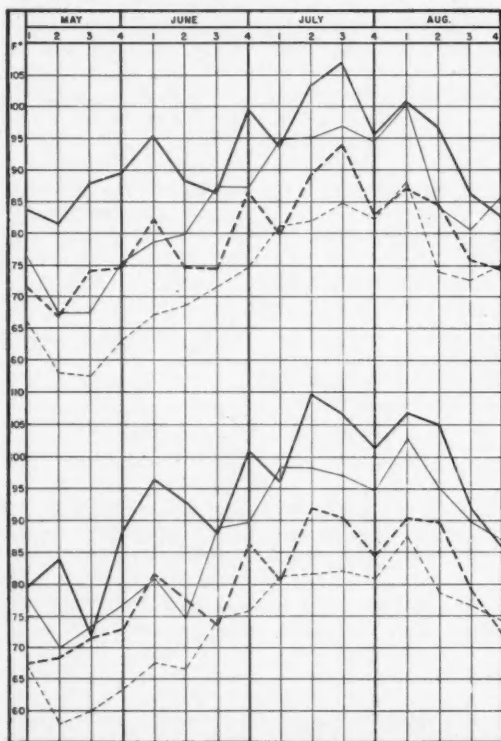


FIG. 29. Average temperatures by weeks at Lincoln, Neb. (UPPER) and Hays, Kan. (LOWER) during a pre-drought year (1930), and one of severe drought (1934). Mean daily temperatures in 1930 are shown by light broken lines and in 1934 by heavy broken lines. Mean maximum temperatures in 1930 are shown by light unbroken lines and in 1934 by heavy unbroken lines.

August. The highest weekly maximum was 109.8°, and during five other weeks the mean maximum temperatures ranged between 101° and 107°.

EVAPORATION

Losses of water from Livingston's non-absorbing, cylindrical, porous cup atmometers are shown for the season 1920 in Figure 30. The data are representative for 1921 and 1922 also, since similar constant differences in the rates of water loss were ascertained. Evaporation was greatest throughout the season at Burlington (23 to 57 cc. average daily losses), intermediate at Phillipsburg (12 to 32 cc.), and least at Lincoln (9 to 25 cc.).

Amounts of evaporation in inches from a free water surface during the growing seasons of 1930 and 1934 are shown for Lincoln and Hays in Figure 31. Even casual examination reveals the very much higher monthly evaporation rates during the dry year. Sometimes they were one-third or more greater than during the predrought year. Extremely high losses occurred during June, July, and August. Unfortunately, evaporation at the two stations cannot be

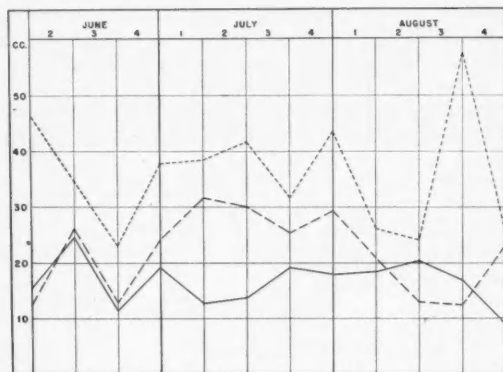


FIG. 30. Average daily evaporation by weeks at Burlington, Colo. (short broken lines), Phillipsburg, Kan. (long broken lines), and Lincoln, Neb. (unbroken line), in 1920.

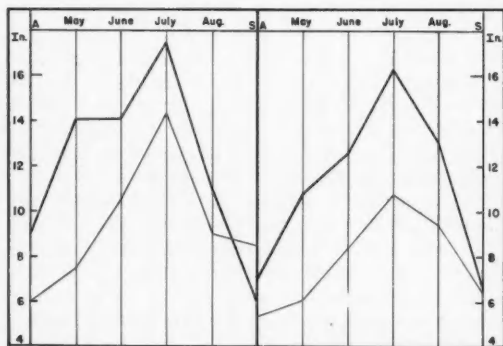


FIG. 31. Evaporation in inches from a free water surface at Lincoln, Neb. (left) and Hays, Kan. (right) in 1930 before the drought (light line) and during the severe drought of 1934 (heavy line).

compared, since data for both years at Lincoln were obtained from the regular Weather Bureau tank exposed 14 inches above the soil surface, and that from Hays from a much larger tank with exposed water surface 2 inches above that of the soil. Data comparable with those at Lincoln (or the reverse) were not obtainable for both years.

In addition to recurrent adverse environmental conditions, trees in prairie are subjected to injury by many kinds of insects, rodents, and other harmful organisms. These were formerly considered as environmental factors, but such activities are best understood as coactions (Fig. 32).



Fig. 32. Coaction between jackrabbits and young honey locusts at Hays. Russian thistles lodged about the trees in this windbreak and caused the snow to drift. When other food was scarce, jackrabbits ate the bark (note white patches of sapwood) and thus caused the death of the trees.

CAUSES AND NATURE OF INJURY

A report has been made by Hursh and Haasis (1931) on the effect of a drought of extraordinary severity in the southern Appalachian region during the summer of 1925. The deficiency of the precipitation was expressed by early browning and premature leaf fall. Most of the trees on good sites apparently recovered completely the following year. On upper slopes and on shallow or rocky soils some trees were severely injured or killed either directly or subsequently through secondary agencies. Partially killed crowns, resulting in stagheaded trees, were of common occurrence on shallow soils. Four years after the drought all trees that had maintained normal foliage during this dry period showed no evidence of injury. About half of the trees showing definite drought injury completely recovered. The remainder sustained injury in the form of dead branches in the crown or were killed by drought or by secondary causes.

Although young trees, even on prairie uplands, may not be retarded in their growth by moisture deficiency during years of good precipitation, trees reach maturity rapidly when the quantity of available moisture in the soil is restricted. After a period of

only 20 to 30 years the vigor of most trees in open mixed-prairie sites begins to decline. Such a condition, even without drought, provides a favorable environment for the invasion of insects and disease-producing organisms. Within 50 years the average planted grove in the mixed prairie will disappear, since here reproduction from stumps or seedlings only rarely occurs.

Unrestricted grazing was found by Kaylor et al. (1935) to be one of the commonest causes of excessive mortality in old timber claims and windbreaks. In nearly all of them there had been grazing at some time or other during the life of the trees. Some were kept free of livestock until the beginning of the drought, when scarcity of regular feed and the necessity for shelter from the terrible heat forced the farmer to open his groves to the stock. This resulted in much trampling and the resultant unfavorable conditions for water absorption. The roots of trees were often exposed, and any seedlings, saplings, or sprouts were eaten, as well as the lower branches of the trees. It has been pointed out by McComb and Loomis (1944) that in western Iowa bur oak in the original prairie on loess soil showed no injury even on severely exposed sites during drought, but heavily pastured bur oak was killed or severely injured. American elm was killed and bur oak injured on a moderately pastured north slope, but no signs of injury were evident in unpastured reproduction on the south slope of the same hill.

The evil effects of grazing wooded areas has only recently begun to be at all fully understood (Day & Den Uyl 1932, Den Uyl, Diller, & Day 1938, and Dambach 1944). Any damage to trees by livestock, jackrabbits, insects, fungi, or other causes makes them more susceptible to injury by severe drought.

Relatively little is known concerning the drought resistance of different species of trees, or of the same species at different ages, except such information as has been obtained empirically by observing whether or not certain trees will survive in a given climate. Shirley (1934) and Shirley and Meuli (1939) have experimented with a desiccating chamber which maintained nearly a constant saturation deficit. Potted seedlings of trees of several species were subjected to desiccation, and relative drought resistance judged by the length of time the trees survived and the water content of soil at death. In nature several factors are involved. A chief one of these in the Midwest is the competition of the tree seedlings with grass. Such competition affects the growth of both roots and tops and results in high mortality of the trees. Root competition for available soil moisture and soil nutrients as well exerts a profound effect upon establishment, survival, and growth of trees, as has been shown by experiments in the prairie near Lincoln, Nebraska.

EFFECTS OF COMPETITION OF GRASSES

For sustained growth, trees require relatively large amounts of water. In a dry prairie climate they grow naturally on alluvial and terrace lands along

streams and on stream banks, and in portected places in rough uplands. These are all places which from time to time are laid bare or have been bared by running water or at least where the prairie grasses cannot invade or where their hold has been broken by natural causes. The establishment of seedlings in upland prairie is extremely difficult because of competition with the grasses for water. On lowland they are shaded by the tall grasses so completely that death usually ensues. These are conclusions not only from observations but from several years of experimentation (Clements, Weaver, & Hanson 1929).

The success of the tree plantations in the prairie has led to the assumption that even the true prairie owes its persistence to fire and that the climatic relations are not controlling. The fact is overlooked that such groves have been artificially aided in a number of ways, such as the destruction of the grass cover, the use of clean tillage or mulches, or actual watering, and the employment of young trees tall enough to escape overshadowing. In short, the most critical time in the whole process, that of germination and establishment, is avoided by the use of transplants, while the physical factors and competitive relations are profoundly modified to the advantage of the trees.

In extensive experimental work on competition of seedling trees with grasses, seedlings of soft maple (*Acer saccharinum*), honey locust, American elm, boxelder, and green ash were grown under four degrees of competition. Four long parallel trenches 4 inches wide and 4 inches deep were made in prairie on low, level land by removing the native sod. They were filled with loose prairie soil free from roots and the seed sown, water being added from time to time to insure germination and establishment. Four degrees of competition were obtained as follows:

1. In the first trench, the sod was overturned to a depth of 4 inches to a distance of 6 inches on either side, and was then thoroughly pulverized to constitute a mulch. Frequent shallow hoeing kept this area free from all vegetation during the following seasons. The overhanging grasses along the edges were kept clipped to insure good lighting and thus confine the competition to the soil.

2. The grass along the second trench was kept clipped to the ground to a distance of 6 inches on both sides. There was practically no competition for light, the demands of the clipped cover for water and nutrients were moderate, and the corresponding competition was not severe.

3. Along the third trench the grasses were watered rather freely from time to time during the first year, and especially in periods of drought. They were not trampled and since sufficient water was present at all times, the competition in this row was chiefly for light and to some extent for nutrients.

4. Trees in the fourth trench were flanked by the grasses of the prairie and were entirely unaided in competition with them.

As a whole, the mortality among the trees increased with the degree of competition. Figure 33 is representative of the relative development; watering caused the grasses to grow more vigorously, with the con-

sequence that the trees received even less light than in the unaided row. Some deaths occurred each year. At the end of the third year the average loss of all trees in the mulched row was 31 percent, in the clipped 62, while it was 79 and 92 percent, respectively, in the watered and unaided rows.

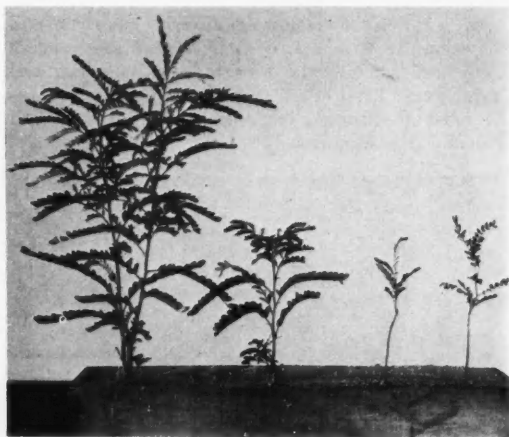


FIG. 33. Representative year-old seedlings of honey locust grown in mulched (left), clipped, watered, and unaided (right) rows. Explanation in text.

Development of the root systems in the third year was directly in proportion to the tops. Depth of the taproot of honey locust after three years was 6.5 feet in the mulched row, 5 feet in the clipped, 1.7 feet in the unaided and watered rows. Branching was profuse in the surface 2 feet, 1 foot, and 0.5 foot of soil in the above sequence. Average lateral spread from the taproot of a great mass of fine roots (nearly all up and down the row) was 4.5, 2.5, and 0.5 feet, respectively.

Results of these studies are in accord with later studies on windbreaks which showed that cultivation of the soil in the arid prairie climate until a complete crown cover was established had a decidedly beneficial effect by reducing the competition from grasses and weeds (George 1943).

Further evidence that competition with grasses is very effective in retarding the development of trees has been obtained by Pearson (1934, 1936, 1942). These studies show conclusively that dominance of grasses retards and may prevent regeneration of forest trees. The fine network of absorbing roots of trees may be quite as dense as that of grasses (Fig. 34).

ROOT DISTRIBUTION IN RELATION TO DROUGHT RESISTANCE

The nature and adaptability of the root system of trees in a manner to obtain the greatest possible amount of soil moisture is a fundamental concept in a study of drought. In an investigation of the invasion of prairie by forest, Weaver and Kramer (1932) pointed out that the invasion of trees into

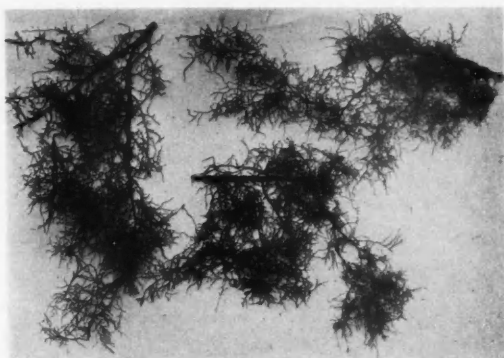


FIG. 34. Fragments of roots of green ash grown in upland, showing the fine network of branches developed in dry soil.

grasslands was primarily a phenomenon of plant competition and that water in dry climates was the chief factor concerned.

Examination was made of the root system of bur oak, a most xeric forest tree, in silt loam soil in eastern Nebraska. A mature tree 37.5 feet tall, 14 inches in basal diameter, and 65 years old, was excavated. The taproot tapered rapidly and extended downward to a depth of 14 feet. It gave rise to 30 or more large main branches, most of which arose in the first 2 feet of soil. Most of the main branches, which varied from 1 to 7 inches in diameter, extended outward 20 to 60 feet before turning downward. Some grew more deeply than the taproot. All branched repeatedly, and together they occupied a very large volume of soil. Many branches of the main lateral roots grew vertically downward 8 to 15 feet, each resembling more or less the taproot system of a young oak tree. Others extended obliquely or vertically upward and filled the surface soil with mats of absorbing rootlets. The weight of the roots equaled that of the top; the volume of the roots was about one-tenth less than that of the parts above ground.

These writers concluded that the scarcity of the water supply, at least during recurrent periods of drought, was the chief external factor promoting extensive root development. They state: "That the adaptation of a species to its habitat is largely a matter of root development is a viewpoint that is being strongly supported by rapidly accumulating evidence." They also state that "although the root habits of a tree are governed, first of all, by hereditary growth characters of the species, they are often quite as much the product of environment."

Holch (1931) examined in eastern Nebraska the development of the root systems of seedlings and saplings of five deciduous forest trees growing in various habitats, including plowed prairie. In former prairie land the taproot of bur oak reached a depth of 4.5 feet the first year and 7 feet the third,

when the wonderfully branched root system occupied a circular area 4 feet in diameter to a depth of 6 feet. Shagbark hickory and red oak, both less xeric species, had somewhat shorter taproots which were less extensively branched. Walnut had a deep and remarkably well-branched root system. That of linden, which is rarely planted westward, reached only 1.2 feet the first year but later its roots spread widely in the surface two feet of soil and a few penetrated to about 5 feet.

Biswell (1935), working in the prairie region of central Missouri, found many important variations in the root habits of trees due to differences in environment. Seedlings of boxelder penetrated into the loess soil twice as far as in clay and almost three times as far as in alluvial soil where growth was greatly retarded by deficient aeration during early summer. The root system of boxelder was found to be very plastic. On upland both taproot and major branches of 5-year-old trees penetrated to a depth of 12 feet. But in alluvial soil of a flood plain the taproot of a 15-year-old tree was only 9 feet deep. Many strong laterals spread outward near the surface of the soil to a distance of 5 to 12 feet. The root system of honey locust was readily modified by environment. In upland soil taproots of 6-year-old saplings penetrated to 5 feet, but on the flood plain to a depth of only 2 feet, and laterals extended outward 10 to 17 feet. The shallowly rooted cottonwood of the flood plains sent its strong taproot deeply in upland soil; a 3-year-old tree reached a depth of 9 feet, but lateral spread was small. Conversely, mature trees growing in sandy soil along rivers where the water table is permanently high, are sometimes blown over by the wind. Then they exhibit a "flat-bottomed" root system, the laterals extending widely but the depth of penetration being shallow.

Such knowledge helps one to understand the behavior of trees in different habitats under the impact of drought. For example, the parents of the first author planted rows of cottonwood trees over a hill-top near Hill City in central Kansas about 1900. Nearly all of these trees, undoubtedly deeply rooted, survived the early years of the drought and did not completely succumb to it until 1939. This was in sharp contrast to the early death of similar trees, which were probably shallowly rooted, growing along a nearby intermittent stream.

Hayes and Stoeckeler (1935), in a study of the relationships between trees and soil in the shelterbelt zone, examined the root systems of 126 trees and shrubs on fine textured and sandy soils. Particular emphasis was given to the depth of root penetration. In general, the vigor and the percentage of survival of trees throughout the well-drained uplands and terraces increased with the sand content of the soils and decreased with the clay content, a phenomenon related to the available moisture supply in both sandy and clayey soils at all times, and especially during droughts. Fine textured soils were not wet deeply; in fact, below 2 to 3 feet these soils never attain

their field-carrying capacity, except possibly in years of highest precipitation. Larger, older, and more drought resistant trees were nearly always found to be more deeply rooted than trees of the opposite description. Except in areas where the ground water lies high the shallow-rooted trees were more subject to serious injury or death during periods of deficient precipitation.

They classified hackberry, honey locust, bur oak, mulberry, and Osage orange as more deeply rooting (10 to 20 feet where soil was moist to these depths). Green ash, American elm, red cedar, and boxelder were of intermediate root depth (5 to 10 feet). Willow, cottonwood, and catalpa were much more shallowly rooted (1 to 5 feet). Their observations indicated that the slower-growing trees have a greater life span in the shelterbelt zone.

A 50-year-old American elm, 45 feet high, was found to be rooted mostly in the first 3 feet of clay loam, but partly in the second 3 feet of silty clay loam. Nearly the entire root system of a green ash 46 years old in silt loam over a claypan had grown in the surface 3 feet of soil. None of the trees best adapted to planting in the Great Plains seemed to be seriously affected by the zone of lime accumulation in the soils, the so-called lime layer. A 50-year-old bur oak was rooted only 8 feet deep in clay loam soil. It had penetrated quite beyond the zone of lime enrichment, which occurred at 2.5 to 3.5 feet. The roots of most trees were more numerous above the zone of lime enrichment, that is, the upper 2 to 3 feet, where such factors as water, aeration, nutrients, and soil organisms are more favorable for growth.

George (1939) states that: "Trees on the northern Great Plains are often comparatively shallow rooted, which is caused by absence of sufficient moisture at greater soil depths. The trees, therefore, must rely largely on current moisture." Yeager (1935), working at Fargo, North Dakota, where the average annual precipitation is 22.3 inches, found that of 31 species of trees and shrubs excavated more than 97 percent of the roots by actual count occurred in the first 4 feet of soil.

DIRECT CAUSES OF INJURY AND DEATH

Death of trees and shrubs on flood plains and terraces sometimes occurred within a few months if the water table lowered rapidly and shallow root systems occurred only in the upper layer of soil. Paradoxical as it may seem, trees in ravines continuously moist before the great drought in general succumbed first while those deeply rooted in the drier upland soil died later, if indeed they did not survive the drought. Where a permanent supply of water was available few or no trees died; in fact, as will be shown, some benefited by a moderate lowering of the water table and concomitant better soil aeration. Injury and death of woody plants due to the effects of drought were often the result of continuous adverse climatic conditions over an extended period of time. The process resulting in drought injury was usually grad-

ual and began long before death actually occurred. Drought injury among trees is doubtless a recurrent condition at least throughout the drier portions of the prairie. It was present in a mild form during droughts of short duration, but became very general and severe during the continued and intense drought of the 'thirties. It was then that destruction became very great.

INJURY TO FOLIAGE

The early signs of drought on the uplands were given by the vegetation beneath the trees, especially those which occurred in open stands. Here there was rolling, folding, or curling of leaves, few or only partially developed flower stalks, and withering and falling of the foliage. As drought continued the density of the herbaceous cover was reduced somewhat in proportion to the decrease in water content of soil, an adjustment to the changed environment which woody plants could not make.

Aside from the wilting, discoloring, or shedding of the foliage already described for early drought, an early outward sign of prolonged drought among deciduous trees was reduction in size and number of leaves. Often, only a half crop of small leaves was produced (Fig. 35). Likewise, defoliation of the



FIG. 35. (UPPER) Osage orange in central Kansas with scant foliage during drought, 1933. (LOWER) The same hedgerow in 1944, showing dense foliage, and sprouts from the bases of some of the old trees.



FIG. 36. Cottonwoods along an intermittent stream in central Kansas which have suffered much damage from drought. September, 1939.

outer portions of the crown was of common occurrence (Fig. 36).

Foliage of trees was often reduced and in many instances almost totally destroyed by grasshoppers, web worms, and leaf-eating larvae of other insects. Such attacks usually occurred during years of great drought when the amount of other green vegetation was limited or had dried completely. The dry weather was favorable for canker worms or web worms which are ordinarily washed from the trees by rains, but during drought trees along the Missouri River and elsewhere were sometimes defoliated two or three times during a single season. When green herbage became scarce or absent on uplands, and not abundant even in ravines, swarms of grasshoppers migrated to the low ground and fed upon the leaves of trees and shrubs. On the hillsides and elsewhere, smooth sumac, for example, was not only defoliated but the bark also was removed from the stems. Such injury was common eastward at least to the Missouri River. Only a few species, such as red cedar, were immune, at least from severe injury. Most trees, shrubs, and woody vines were considerably damaged and some were completely defoliated. On certain introduced species, especially Colorado blue spruce (*Picea pungens*) and tamarisk (*Tamarix* spp.), grasshoppers were at times so numerous, at least locally, that the foliage was scarcely visible. Not only the leaves but also the bark of the twigs and small branches were eaten; this resulted in the death of the spruce but not of tamarisk, which sprouted from the base. Trees in timber claims and windbreaks also suffered heavily early in the drought; later they presented less foliage, but injury by grasshoppers continued heavy on moist lowland. On numerous occasions some deciduous trees were entirely defoliated by grasshoppers, leaf beetles, blister beetles, or other leaf-eating insects.

INJURY TO BRANCHES

When the foliage was reduced in amount by whatever cause, the branches were exposed to high insolation during periods of great heat and low humidity. This was probably a cause of much direct injury (Fig. 37). Desiccation resulted in death of the tips of branches, sometimes rather generally but most usually in the tops of the crowns. This permitted the entrance of wood borers of various genera and species, or other insect larvae, as well as fungi, into the dead or partially dead wood. Death of the tree often proceeded rapidly from the tips of the branches toward their base through the combined influence of desiccation and wood borers. If soil moisture was restored before death was complete, deterioration was slowed or stopped and often growth was resumed from the living branches.



FIG. 37. Interior of a woodland of shagbark hickory (*Carya ovata*) near Nehawka in eastern Nebraska. Before the drought this forest of 35- to 45-year-old trees was in good condition, but in 1943 scarcely an uninjured tree was found.

Infestation by wood borers undoubtedly aided drought in injuring or in causing the loss of many trees by death. Examination of the wood of honey locusts at Hays by cutting sections of the trunk and large branches at different heights revealed that the number of wood borers increased downward from the parts that had recently died. They were present at a distance of several feet from the partially dead wood.

RECORD OF LOSSES

Throughout the years of drought while the writers were studying the destruction of grassland (Weaver

& Albertson 1936, 1940, Albertson & Weaver 1942, 1944), and finally its recovery (Weaver & Albertson 1943, 1944), considerable attention was given to the losses of both native and planted trees and shrubs. Because of the arduous and extensive work on grassland, time for a record of losses of trees was limited. It was confined largely to the western half of Kansas, although many observations and counts of dead trees were made elsewhere. The method consisted in an actual count of all standing trees living and dead that were found in dry ravines, in the protection of bluffs, along intermittent streams, and more abundantly along continuously flowing streams or about springs. Much study was also given to trees planted as groves or timber claims, windbreaks, and hedgerows. In nearly all, the counts were made early in the drought years and again several years later. Thus, a large amount of factual data has been obtained.

DESTRUCTION OF NATIVE TREES AND SHRUBS

The native trees in the area are typically representative not only of the farthest westward extension of deciduous forest into the dry prairies but also they illustrate in general similar conditions southward in western Oklahoma and northwestern Texas. Westward on the plains of Colorado woody growth, if present, is even more sparse. To the northward in the hardlands of Nebraska and the Dakotas conditions similar to or even more adverse than those in Kansas prevail, except here ponderosa pine is found in addition to the far western outposts of deciduous forest (Kellogg 1905).

LOSSES IN DRY RAVINES AND ON STEEP BLUFFS

Extensive areas of the Great Plains are characterized by rolling hills with dry ravines, which receive runoff water, extending far back from the streams into the uplands. Except for the level uplands where trees do not occur naturally, the dry ravines are the most xeric sites in which woody vegetation is found. Sometimes trees occur only as individuals. They are always found most abundantly near the bases of the north-facing slopes. But where the slopes are steeper and some seepage through underlying rock occurs, both lower slopes may support them. Trees in many such ravines have been studied; typical results are shown in Table 2.

An examination of Table 2 reveals that early losses of hackberry (4 to 7 percent) were much lower than those of American elm (16 to 27 percent).³ Although losses of both species increased greatly with the continuation of drought those of hackberry (48 percent) were still far less than those of elm (76 percent). On the south-facing slope all of the elms and three-fourths of the hackberry had died by 1939. It was more sparsely populated and the trees survived for a longer time probably because they were more deeply rooted. In all sites death of hackberry was consistently less than that of elm. Of a total of 20 elms and 32 hackberry trees growing in a ravine

³ *Ulmus americana* is the only species of elm growing naturally in the region. Hereafter it will be designated simply as elm. Likewise, green ash (*Fraxinus pennsylvanica lanceolata*) will be called ash.

TABLE 2. Loss of native trees in ravines near the Saline River at Hays, Kansas.

Species	Year	Habitat	NUMBER OF TREES		Percent Loss
			Living	Dead	
American elm.....	1935	South-facing slope...	26	5	16
	1935	North-facing slope...	237	90	27
	1939	" " " " " " " "	78	249	76
Hackberry.....	1935	South-facing slope...	22	1	4
	1935	North-facing slope...	153	11	7
	1939	" " " " " " " "	86	78	48

4 miles west of Hays, three-fourths of the elms had died by 1938 but only one-fourth of the hackberry trees (Fig. 38).



FIG. 38. Typical dry ravine on rocky soil in natural grassland near Hays, showing condition of elm and hackberry in the spring of 1939.

A few miles east of Woodward, Oklahoma, observations were made in May 1938, of trees growing on north-facing slopes. Many of the tops of elms were badly damaged by drought and wood borers. Farther up the protecting slopes, many of the trees had died and the remainder were seriously damaged.

In ravines formed by cutting through loessial or glacial deposits, limestone formations are absent, hence the trees in these locations are firmly rooted in deep rich soil. Lateral seepage, however, is as common here as in the limestone outcrops. It has been estimated by Bennett (1939) that the water table was lowered as much as 20 feet in some places in the Great Plains by gullies cut through the substrata. Under these conditions much of the vegetation, including scattered trees and shrubs, was unable to survive on the limited rainfall.

Studies made north of Osborne, Kansas, in ravines on the highland indicated that elm and hackberry had been reduced to less than one-third the original number. In the fall of 1939, ravines along the Smoky Hill River 60 miles southeast of Hays were studied to determine the nature of growth and drought injury. The trees were mostly elm, hackberry, ash, and cottonwood, but occasionally bur oak. Even in this more mesic habitat nearly 50 percent of the elm and bur oak were dead; the others suffered somewhat less.

In a ravine in a buffalo grass pasture about 9 miles south of Superior, Nebraska, much destruction had occurred to bur oak. The trees grew in a loam soil underlaid with limestone. Where the soil was deepest they were 28 feet tall and 8 to 12 inches in diameter. But on the rocky slopes a height of only 20 feet and a diameter of 5 to 7 inches were attained. All were dead or badly injured (Fig. 39).



FIG. 39. Bur oak in the upper portion of a dry ravine near Superior in south-central Nebraska, showing great destruction by drought.

On steep north hillsides at Weeping Water, in eastern Nebraska, where the soil was also underlaid with limestone, a mortality of 80 percent was suffered by red oak, as well as by the linden near the base of the slope. Many other trees and shrubs also succumbed (Fig. 40).

In a large prairie near Alma in south-central Nebraska, the mortality rate of elm was extremely high; in some places all had died (Fig. 41). Near Lincoln in eastern Nebraska trees of elm and ash in a ravine running through a large prairie had lost half their number by 1939. The remainder had suffered considerably as was indicated by the numerous dead branches in their tops. Young trees and shrubs showed less injury from drought than did the older ones. Similar losses in shallow ravines and on slopes in southwestern Iowa have been observed. Indeed, such losses were widespread through much of the true and mixed prairie.

The shrubs near Hays, limited generally to ill-scented sumac, snowberry, and smooth sumac, experienced a high mortality, especially when growing together in dense clumps. It was not uncommon to find large communities of these shrubs on exposed slopes which, except for a few small plants, had succumbed to drought. Shrubs on north hillsides suffered much smaller losses (Fig. 42).

In ravines along which runoff water finds its way into the streams there occurred depressions or pockets which thus receive a supplementary water supply. Here sometimes were found thickets of wild plum, some of which had suffered greatly from drought. Many were entirely buried under the drifts of dust. Elsewhere the dust had accumulated to a depth of a few inches to several feet. This contributed greatly



FIG. 40. Injury to red oak and to linden (center) growing near Weeping Water at the foot of a steep north-facing slope where the other trees were all destroyed by drought. May, 1944.



FIG. 41. Shallow ravine near Alma in south-central Nebraska in which American elms were all dead in August, 1939.

to their death, for so poorly did the rain water penetrate the dust that the soil in which the plums were rooted often remained dry. This phenomenon was not local but occurred eastward at least as far as the Missouri River.

Trees were usually more abundant near the base



FIG. 42. Steep, rocky, north-facing slope with ill-scented sumac. Note the dead bushes at the left near the top of the hill.

of steep bluffs than on the higher slopes or below the base of the bluffs on more level land away from the "seeps" between the rock strata. The mortality rate in these locations depended greatly upon the exposure to the sun and desiccating winds (Table 3).

TABLE 3. Death of trees on steep slopes 16 miles north of Hays in June, 1935.

Species	Habitat	NUMBER OF TREES		Percent Loss
		Living	Dead	
Red cedar.	West exposure.....	28	2	7
" "	North exposure.....	39	0	0
" "	Northwest exposure	28	0	0
Elm.....	Northwest exposure	48	22	31
Ash.....	Northwest exposure	19	11	37

Even in the best protected sites there were definite signs of drought. Many of the leaves of red cedar had fallen and formed a brownish litter beneath the trees. Dead branches were common.

A much larger area in this locality was examined three years later. Losses of red cedar had increased to 35 percent; death of hackberry and ash were 31 and 43 percent, respectively, but loss of elm was 93 percent.

TABLE 4. Losses of trees on a steep bluff 16 miles north of Hays in August, 1938.

Species	NUMBER OF TREES		Percent Loss
	Living	Dead	
Red cedar.....	328	175	35
Ash.....	363	276	43
Hackberry.....	91	40	31
Elm.....	8	101	93

The shrubs found in this locality in 1935 were definitely affected by drought. At least 90 percent of ill-scented sumac and snowberry had succumbed. In fact scarcely any remained except those that were

growing in small depressions. The sparse population of smooth sumac, however, had sustained only slight loss.

Red cedars on a north-facing bluff on the Smoky Hill River 30 miles southwest of Hays suffered more from drought than in any other site. In 1937, 60 percent were dead, and two years later the death toll had increased to 80 percent (Fig. 43). Sixty miles east on a less xeric north-facing bluff, the average loss of red cedars did not exceed 10 percent. But locally, especially where the trees extended above the brow of the bluff, large numbers had died (Fig. 44). Here the deciduous trees (elm, hackberry, ash, and cottonwood) showed the same low mortality. But on higher land beyond the rocky outcrop, where the roots were unable to obtain moisture from the "seeps" between the layers of rock, the loss was considerably greater. Studies on a similar site near a small stream north of Russell revealed 1 percent loss of red cedar and 10 percent each of ash and hackberry, but all of the elms had died.

Summarizing, the average percentages of losses in



FIG. 43. Native red cedars growing in the shelter of limestone cliffs in central Kansas. July, 1939.



FIG. 44. Old, gnarled red cedars near the brow of a steep north-facing bluff 20 miles northeast of Hays. October, 1939.

ravines late in the period of drought were, approximately, elm 70 and hackberry 36. On bluffs, percentages of losses were red cedar 37, elm 56, ash 33, and hackberry 28. The loss of red cedar was high in comparison with that of deciduous trees due to its great loss (80 percent) on a dry bluff where no other species were found.

LOSSES ALONG INTERMITTENT STREAMS

Many streams in western Kansas had only an intermittent flow of water even during years of normal precipitation. The source of this water was runoff from the surrounding higher land or seepage from hillsides following heavy rain. During the drought years the streams were usually dry in summer. The general lowering of the water table left the roots of the trees quite above a continuous water supply. Mortality along such streams was high (Table 5).

TABLE 5. Losses of trees along a small stream near Hill City, Kansas.

Species	Year	NUMBER OF TREES		Percent Loss
		Living	Dead	
Cottonwood	1935	80	78	49
	1939	28	130	82
Peach-leaved willow	1935	17	98	85
	1939	5	110	96

The water in this stream had cut through sandy soil and flowed over a layer of shale. There were approximately 300 trees, mostly cottonwood and peach-leaved willow, along a half mile of this stream. Hackberry and elm were found on the steep bluffs some distance from the creek. The first study was made in 1935 after three years of continuous drought. The water table had been lowered sufficiently to leave most of the roots of the trees in dry soil. Of 158 cottonwoods 49 percent had died. Death toll of willows was 85 percent. Even among the living trees numerous dead branches occurred in their tops. As the drought continued the losses became greater. By the autumn of 1939 the mortality of cottonwoods had reached 82 percent, and that of willows was 96. In similar sites along other streams losses were fully as great; in some places, however, where the trees were protected from desiccating winds, a much larger percentage survived the drought. The loss of cottonwoods varied greatly with the distance above the bed of the stream, as is shown in Table 6.

Of a total of 307 trees 211 died. The greatest loss (98 percent) occurred where the trees were growing well above the stream. On the flood plain where the trees were shallowly rooted a loss of 62 percent was found. This was probably a result of the rapid lowering of the water table. Smallest losses (9 percent) occurred in the intermediate site. Destruction of shrubs along dry and intermittent streams was usually high. Rough-leaved dogwood and wild plum espe-

TABLE 6. Mortality of cottonwoods near a small stream west of Hill City in October, 1935, after three years of drought.

Habitat	Height above bed of stream	NUMBER OF TREES		Percent Loss
		Living	Dead	
On knoll	20 feet	4	168	98
In valley	12 feet	70	7	9
On flood plain	6 feet	22	36	62

cially were injured, also wild currant and indigobush were harmed to a smaller degree.

Observations made along the Solomon River near Woodston in 1938 revealed that approximately 45 percent of the cottonwoods and willows growing near the river were dead. Elm and hackberry, which usually grew farther back from the stream, lost about 75 percent.

Similar observations were also made along streams near Grand Island, Nebraska, in 1938. Approximately 50 percent of the trees were dead (Fig. 45). Large numbers of dead elms were also found on the river terraces near Missouri Valley, Iowa. Cottonwoods and willows growing on the flood plains and thus nearer the water table had suffered relatively small losses.



FIG. 45. Destruction of trees by drought along the banks of Salt Creek 12 miles south of Lincoln. The trees are mostly ash and elm 40 to 50 feet high, with native bluestem prairie in the foreground.

On sandy streams such as the Smoky Hill River near Hays, losses were comparatively light (Fig. 10). Here most of the trees were cottonwood and willow and they seldom attained large size before they were washed away by floods, hence their age was considerably less than that of the trees growing along streams flowing through a heavy soil. The percentage of loss due to drought was negligible on the flood plain but often great farther from the river.

LOSSES ALONG CONTINUOUSLY FLOWING STREAMS AND ABOUT SPRINGS

Streams in which there was a continuous surface flow of water during drought were few in this western

area. Studies of mortality of trees along Walnut Creek near Rush Center were made in August, 1938, and in September of the following year. Occasionally a dead tree was found near the water's edge in the midst of many thriving ones, but the most common sign of drought was the dead branches in the tree tops. Here elm, hackberry, and ash occurred rather abundantly, and cottonwood and boxelder more sparingly. Death of trees was limited to about 2 percent.

On Big Creek 10 miles southeast of Hays, losses were much higher. The stumps in the foreground of Figure 46, where dead trees had been removed, supplied mute evidence of the desiccation that occurred along this stream, where the flow of water although continuous during the drought was greatly reduced in volume. Death of trees varied greatly but the average was about 10 percent.



FIG. 46. Hackberry, American elm, and green ash along Big Creek southeast of Hays where loss by drought was only 10 percent. Most of the dead trees had been removed.

Along Pawnee Creek 12 miles west of Larned, Kansas, and 30 miles farther south on the Medicine Lodge River near Wilmore, a count of trees in 1938 revealed a loss of approximately 5 percent. They were elm, hackberry, and black locust. But many of the tops of the living ones had numerous dead branches.

Farther southwest, on the Canadian River in the panhandle of Texas, cottonwood, hackberry, and elm formed an irregular belt on both sides of the stream. Here relatively small losses were found even as late in the drought as the spring of 1938. Doubtless some dead trees had been removed, but the damage was generally limited to scattered dead branches in the crowns.

Summarizing, average losses in percentage of trees along continuously flowing and intermittent streams were as follows: elms 5 and 62, hackberry 5 and 75, and cottonwood 6 and 59. Along intermittent streams loss of willow was 70 percent. Along continuously flowing streams black locust lost only 5 percent.

Death of trees growing near running springs was rare. Usually the only apparent damage was re-

vealed in their tops, particularly near springs with a sufficient flow to continuously maintain a high water table. Other springs that became mere seeps were unable to supply sufficient water to support trees during the most intense drought (Table 7). In 1942, after two years of above-normal precipitation following seven years of drought, the loss of willows was 89 percent and that of cottonwoods 55.

TABLE 7. Number of living and dead trees and percentage of loss of each species near a spring at Hill City.

Species	Year	NUMBER OF TREES		Percent Loss
		Living	Dead	
Willow.....	1935	37	0	0
	1942	4	33	89
Cottonwood.....	1935	137	3	2
	1942	63	77	55

DESTRUCTION OF TREES IN TIMBER CLAIMS, HEDGEROWS, AND WINDBREAKS

During the latter part of the nineteenth century, many of the pioneers obtained a tract of 160 acres of land from the Federal Government by complying with the provisions of the Timber Culture Act of 1873. Usually 10 acres of land were broken and planted to trees 6 to 9 feet or more apart in rows 6 to 9 feet distant. The soil in these claims usually was cultivated 8 to 10 years until the trees were well established, after which often they received no further care. Severe losses occurred during the dry periods previous to 1933. It remained, however, for the recent drought to almost annihilate the survivors (Figs. 47 and 48). As many as 24 timber claims were examined in a single day, and practically without exception all trees were dead. Occasionally, however, a few half-dead trees remained in the lower places where they were kept alive by run-in water from the higher land (Fig. 49). Although Osage orange



FIG. 47. Destruction of trees in a grove about 50 miles west of Lincoln. July, 1935.

(*Maclura pomifera*) was the tree most commonly found in timber claims, it was not unusual to find the remains of black walnut, black locust, honey locust, ash, and catalpa.

When cultivation of timber claims was discontinued, the ground was readily occupied by an understory of vegetation. The first plants to invade were weedy annuals such as sunflower, lamb's quarters, and pigweeds. These annuals were gradually replaced by perennial plants such as sand dropseed, western wheat grass (*Agropyron smithii*), and goldenrod (*Solidago mollis*). The competition for water by a rather dense cover of grasses and forbs was sufficient to cause considerable loss among the trees. Frequently posts for fence construction were obtained by cutting some or all of the trees of Osage orange a short distance above the ground. Usually a large number of sprouts developed from the remaining stumps and formed a shrub-like growth.

Although great variations in losses were found, due to differences in soil, topography, and kind of trees, data given in Table 8 are representative. Death of the ash (86 percent) was much greater than that of

Osage orange, where only 45 percent succumbed. But later in drought all trees of both kinds died.



FIG. 49. Timber claim 6 miles north of Hays showing death of trees except in low ground. Undoubtedly death was due in part to injury from grazing and trampling. September, 1940.

In general, the greatest losses occurred on the higher land. Often timber claims originally contained several hundred trees of Osage orange. Some were cut for fence posts, but sprouts grew from the base before the onslaught of the drought. After seven years of extreme desiccation, however, few or no trees remained alive except those favored by run-in water.

Opinion of early settlers who witnessed both the planting and deterioration of timber claims in this region was that Osage orange was the most drought resistant of all the trees planted. Catalpa, which is now rarely seen, was the first to succumb; it was followed by black locust and ash.

Where timber claims were located on lowland, the trees survived the drought much better. This is illustrated by a tree claim near Hill City (Table 9). There was no loss of honey locust in 1935, although a few trees did die later in the drought. But black locust lost three-fourths of its numbers early in drought; death among the cottonwoods was only 14 percent.

A hedgerow is simply a row of trees along the roadside or between fields. The use of this name in the prairie, where it is locally termed hedge fence, was probably derived from the very extensive plantings of "hedge" or Osage orange for this purpose. Frequently they are found on both sides of the roadway. The trees were always planted closely; usually this



FIG. 48. (UPPER) A timber claim of black locust (*Robinia pseudoacacia*) near Ogallah, Kansas, August, 1942. The trees were given good care for a number of years and have survived the drought much better than those in most similar timber claims. (LOWER) Timber claim near Hays, October, 1939. The ground had not been cultivated for many years, hence the Osage orange died early in drought. Stumps in foreground that hold the wire are what remain of honey locust that died before the drought.

TABLE 8. Loss of trees on timber claim near Wakeeney, Kansas.

Species	Year	NUMBER OF TREES		Percent Loss
		Living	Dead	
Ash.....	1935	25	158	86
	1939	0	183	100
Osage orange....	1935	88	73	45
	1939	0	161	100

TABLE 9. Percent loss in a lowland tree claim near Hill City.

Species	Year	NUMBER OF TREES		Percent Loss
		Living	Dead	
Black locust...	1935	37	113	75
Cottonwood...	1935	87	14	14
Honey locust...	1935	12	0	0

spiny hedge made a fence unnecessary. Since honey locust and black locust were likewise planted closely, competition for water usually retarded their growth and in the western half of Kansas a height of only 15 feet was common (Fig. 50). Eastward, however, they attained at least twice this stature.



FIG. 50. (UPPER) Ash hedgerow near Bird City in northwestern Kansas. Recovery was limited to a few trees in a depression (right) where they had survived the drought. (LOWER) Hedgerow of Osage orange near Belleville, Kansas, where all of the trees have died. Total loss was common in the central and western parts of both Kansas and Nebraska.

Trees in hedgerows suffered about the same fate as did those in timber claims. Dead trees were usually scattered throughout before the drought began, and by 1935 as many as 75 percent had died in the most exposed sites. The loss increased, however, and during the autumn of 1939 scarcely a living tree was found. Life remained in the lower branches of only a few; these survivors usually were on low ground.

A hedge of approximately 400 trees near Carneiro, 80 miles east of Hays, suffered a mortality of 38 percent in 1939, but there was no further loss (Table 10). A few miles distant, near Ellsworth, the loss among 3,200 trees was 99 percent. Mortality in a hedge near Ogallah, 25 miles west of Hays, was 88 percent, and 91 percent loss was found in one north of Stockton.

TABLE 10. Losses in hedgerows of Osage orange, September, 1942.

Location	NUMBER OF TREES		Percent Loss
	Living	Dead	
Near Ellsworth.....	15	3,185	99
Near Carneiro.....	249	152	38

About 120 miles northeastward near Mankato, Kansas, the death toll was fully as heavy in many places as farther westward. Most of the hedgerows on upland suffered heavily in early drought and by 1939 many were completely dead. Osage orange also suffered considerable damage in central and eastern Kansas and Nebraska.

The loss of trees in windbreaks was extremely heavy unless the soil was cultivated or irrigated. The dust storms of 1935 contributed greatly to this loss through partial burial of the lower parts of trees in great drifts of loose soil. Sometimes these drifts were 4 to 8 feet deep and consequently covered many branches (Fig. 51). Not only did the compacted soil damage parts of the trees by interfering with aeration, but water could not penetrate through the dust to the soil about the roots.



FIG. 51. Windbreak of honey locust in central Kansas which died soon after the dust storms of 1935. Drifts of dust 4 to 6 feet high covered the lower portions of many of the trees.

In a windbreak near Dighton trees had been planted in 1893 and had been given little care until after the drought was well advanced. All but a few of the deciduous trees (ash, elm, and others) had died, but red cedars were still growing in the fall of 1939 (Fig. 52).

On high ground south of Medicine Lodge, Kansas, 90 percent of the honey locust were dead in May, 1938. Three-fourths of the elm had died, and the remainder had much damaged tops.

At Alva, Oklahoma, all the elm and hackberry in some windbreaks were dead; in others mortality was at least 50 percent. Farther west at Perryton in the panhandle of Texas, the windbreaks were few and small, but the loss was not so great as farther north

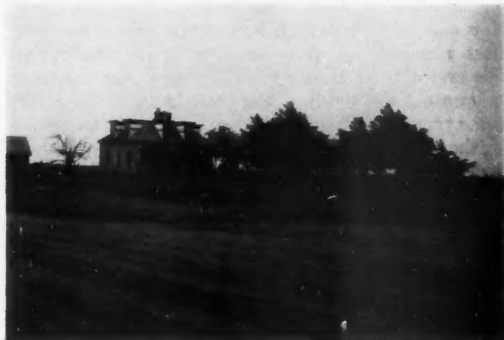


FIG. 52. Farm in western Kansas where nearly all the deciduous trees in a timber claim have died, and only a few red cedars, planted in 1893, are still alive. September, 1939.

near Liberal, Kansas, where 80 percent or more of ash, honey locust, and black locust were dead.

Windbreaks near Kearney, Nebraska, suffered a similar fate to those south of Hays. A few half-dead trees were found in some. Piles of dead trunks cut for firewood were all that remained of many windbreaks that formerly furnished much protection from the cold, north, winter winds.

Observations in western Iowa in 1938 showed that many windbreaks located on high land had suffered much damage, and "hundreds of thousands of adapted trees on suitable or even protected sites were killed or very severely damaged" (McComb & Loomis 1944). In eastern South Dakota a loss by drought of half of the trees in windbreaks was usual.

In summarizing losses it may be pointed out that those which occurred early and mostly after the first extremely dry year (1934) have already been recorded. With ensuing dry years and an accumulating moisture deficit (which was 25 to 34 inches of rainfall at many stations) both injury and mortality increased. It seems probable that in Nebraska and Kansas an average of at least 50 to 60 percent of the trees (aside from young shelter belts) died, and half of the remainder sustained great to moderate injury. Even near the Missouri River entire plantations were destroyed, forests on protecting slopes (nearly all of which were grazed) suffered losses as high as 90 percent, and flood plain trees died in enormous numbers with the lowering of the water table. Red cedar, hackberry, bur oak, and honey locust rank high among trees that endured drought. Silver maple, black locust, boxelder, and cottonwood were less successful in enduring the long periods of desiccation.

RECOVERY FROM DROUGHT

Although there was a return to normal precipitation over much of the prairie area in 1940, drought as measured by recovery of both herbaceous and arboreal vegetation continued still another year. This

interval was necessary, as has been shown by Weaver and Albertson (1944), to moisten the parched soil. Over much of the mixed prairie water penetration was confined to a depth of 3 feet even in 1941. Trees and shrubs that retained some life at the close of the drought usually remained alive for a time unless infestation by wood borers was so complete or the trees so nearly dead that they were unable to resume growth even under favorable climatic conditions.

RENEWED GROWTH WITHIN THE CROWN

Recovery was shown principally and most commonly by renewed growth within the crown. This was usually local but sometimes general. Most of the trees in the driest sites, as in dry ravines, were either killed outright during drought or their living tissue was reduced to a small amount. In many places only an occasional branch had any leaves, especially during the later years of this great period of desiccation. When moisture was again available growth was initiated in those branches and twigs where some living tissue still remained. Even after three or four years of favorable environment leafy branches were often so few and the foliage so sparse that the trees produced very little shade (Fig. 53).



FIG. 53. Drought-stricken American elm growing in a dry ravine near Hays, showing the sparse foliage produced even after the drought. September, 1944.

This greatly retarded the return of the mesic grasses and forbs which formerly grew in the shade beneath scattered trees. In fact, there was little vegetation of any kind. Hence, even where the slope was moderate, there was much runoff and considerable erosion. In less xeric places where injury was not so great a new and complete cover of foliage was soon developed. This phenomenon was especially pronounced in hackberry (Fig. 54).

Trees growing in dry drainageways which received considerable runoff water often resumed vigorous growth. For here much of the lower portion of the trees retained some life. Foliage of the renewed part of the crown was unusually dense. This probably resulted from an abundant supply of water, nutrients,

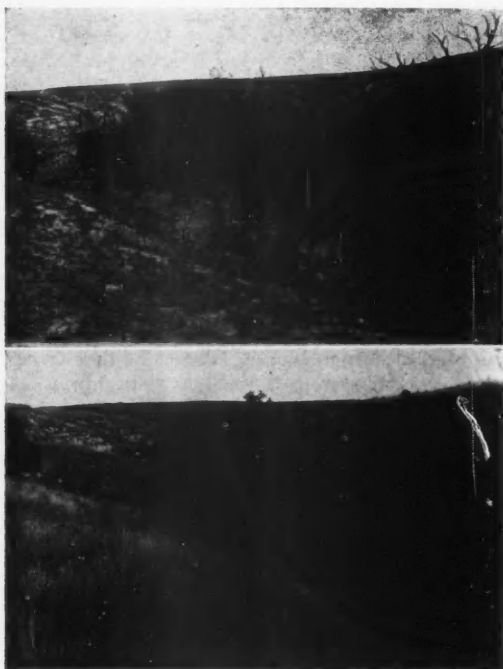


FIG. 54. (UPPER) Group of trees, mostly hackberry, in a ravine at the foot of a north-facing slope near Hays in 1939, showing very sparse foliage. (LOWER) Same view in 1942 after three years of good precipitation.



FIG. 55. Ash, boxelder, and elm in a shallow ravine near Lincoln in 1942. More than 50 percent of the trees were dead. Others renewed growth from the live wood and unusually dense foliage may be seen.

and perhaps accumulated food for these parts, since the roots were apparently not reduced in proportion to the crown (Fig. 55). Similar renewal of growth was found over a wide territory.

In sites less exposed to drought, as on protected, steep, north-facing slopes, recovery began early and

progressed rapidly. Where only the upper part of the crown had died, rapid growth soon hid from view many of the dead branches and only the uppermost remained as witnesses to a great catastrophe. The crowding of the very leafy new shoots presented an unusual appearance; the trees had lost their former symmetry of branching and graceful spreading of the crowns (Fig. 56). Many depressions along highways were occupied by a moderately dense growth of trees, especially cottonwood. Those on the lower ground that survived the drought made rapid recovery by renewed growth within the crown. The conditions of growth when drought was most severe in the fall of 1939 and that after five years of recovery are shown in Figure 57. The foliage was so dense in 1944 that no effects of drought could be seen in the trees in the lowest places.

Trees on Sweet Water Creek, an intermittent stream 14 miles northeast of Hays, responded to a better environment in much the same manner. The trees in the most xeric sites had died whereas at least parts of those in the wetter places had survived. Elm suffered less deterioration than did the cottonwood, hence renewed growth was generally distributed throughout its branches. Conversely, the cottonwood had foliage only in the lower part of its crown (Fig. 58).

Even along the better watered streams recovery by growth of tops was common as late as 1944. While the water in such streams probably never failed completely, yet because of the lowering of the water table some trees died and many of the remainder suffered some damage.

Recovery in tree claims was almost entirely limited to renewed growth of tops or to sprouts from the base of the trees (Fig. 59). Recovery in a timber claim of ash in eastern Colorado is shown in Figure 60. Most of the trees were dead but in some life



FIG. 56. Renewed growth in tops of green ash (left) and American elm (center) on a steep north-facing slope near Stockton, Kansas, in June, 1944.

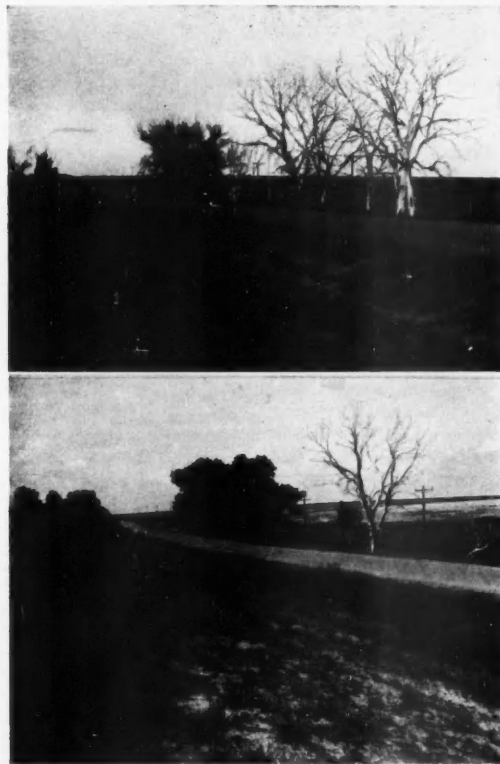


FIG. 57. (UPPER) Large cottonwoods on low ground near Wakeeney in west-central Kansas. Only trees on the lowest ground survived. September, 1939. (LOWER) Same view in 1944. Most of the dead trees had been removed, but those that survived, some of which were 65 years old, produced a dense foliage which hid from view many of the remaining dead branches.



FIG. 58. Trees along an intermittent stream near Hays. Note the dense foliage of the elm (left) and on portions of the cottonwoods that remained alive.



FIG. 59. Remnants of a timber claim on level lowland near Broken Bow in central Nebraska. Abundance of buffalo bur (*Solanum rostratum*) and other weeds indicate much grazing and trampling. The green ash which were not dead showed life only in the lower portions of their crowns.



FIG. 60. Remnants of an extensive timber claim on hard land east of Cope, Colorado. Nearly all of the trees remaining in 1943 were dead; a few had dense foliage, mostly in the lower branches.

still persisted in portions of the crown. In many trees the foliage was so dense that the general appearance was that of witches' brooms.

Many of the trees with only a few living branches will probably survive but a very few seasons even with the best environmental conditions. Few could

endure another period of drought. How long those with moderate injury to the crown can survive cannot be foretold.

In hedgerows on high land in the western half of Kansas trees that had suffered little injury were rarely found; a few had only an occasional green branch; nearly all were dead. In trees that did survive, revival of growth was slow, especially in the Osage orange, and even after three years of recovery no great change had occurred.

On the lowland, where drought was less severe, renewal of growth was rapid when a favorable environment again prevailed. During drought the foliage was sparse but well distributed throughout the crown. Later it not only became thicker but actually denser (in 1944) than normal foliage before the drought.

RECOVERY BY BASAL SPROUTS OR REPLACEMENT BY SEEDLINGS

A second but minor method of recovery was the production of sprouts from the base of the trunk if it remained alive, or from the stumps of such trees that had been removed for firewood. Many such sprouts grew rapidly and in 2 to 3 years had attained, even in the more arid regions, a height of 5 to 10 feet. Sometimes root sprouts developed, especially from trees growing on steep banks and slopes, where many roots had become exposed by soil erosion. Initiation of root sprouts was often due to injury resulting from trampling by cattle. In any instance these new shoots seemed to be well supplied with water and their early growth was very rapid.



FIG. 61. Reproduction by seed of hackberry and elm about large trees that died as a result of drought and were removed. Fifty annual rings were counted in the stump in the foreground. The site is a north-facing slope near Stockton, Kansas.

A third method of recovery of woody vegetation was the replacement of dead trees by seedlings. Seedlings of any species of tree were found only where the trees were growing naturally, and never in great abundance. They were not found in timber claims,

windbreaks, or hedgerows in mixed prairie and in only a few of the best old timber claims eastward nearly to the Missouri River. Almost all of the old timber claims were being grazed or had been pastured. Grazing and trampling is always inimical to growth of trees. Seedlings have played an important role in restoring woody vegetation, especially among the native trees in ravines, on steep slopes, and along intermittent streams. In many of these locations, after the drought great numbers of small trees 6 inches to several feet in height were scattered about in the open spaces left by the death of the parent trees (Fig. 61). Many young trees of hackberry and elm were becoming established on north-facing slopes. The older ones had probably begun growth before the death of the parent trees. Red cedars continued to replace their losses throughout the drought. In fact, there is considerable evidence that this species is not only replacing its losses but actually extending its area of occupation. Seedlings were often most numerous on steep slopes and in fence rows where livestock were excluded.

EFFECT OF CHANGING ENVIRONMENT ON GROWTH

In order to ascertain the effect of drought upon the rate of growth, a study was made of the annual radial increment of the uninjured or least injured trees. A comparison of total increase in radius during the 8 wet years (5 preceding and 3 following the drought) with that of the 8 dry ones has also been made. That the years 1928 to 1932, and 1941 and 1942, had relatively high precipitation may be seen even by casual examination of Figure 62. The intervening years were all either extremely or moderately dry.

An increment borer was used to obtain cores of wood, 3 feet above the soil, from the different species of trees found growing in various sites. At each sampling station cores were taken from each of 3 to 8 trees (except in rare cases where only 2 trees were found) in dry, intermediate, and wet habitats. All the stations were in the western half of Kansas. The habitats classed as dry were the driest that could be found in each location, such as dry ravines and drainage channels. Almost without exception the soil was underlaid at some depth within the zone of root distribution by bedded limestone. Those classed as wet were the most moist, such as stream banks and places near living springs. The intermediate habitats were intermittent streams where the water table had been lowered during the dry years.

Hackberry, elm, and ash were the trees most commonly sampled. Southwestward, however, cottonwood was frequently the only species found. Osage orange was sampled only in hedgerows, most of which had been planted on dry upland. Some hedgerows, however, extended across ravines. Here it was possible also to obtain cores from trees growing in intermediate habitats.

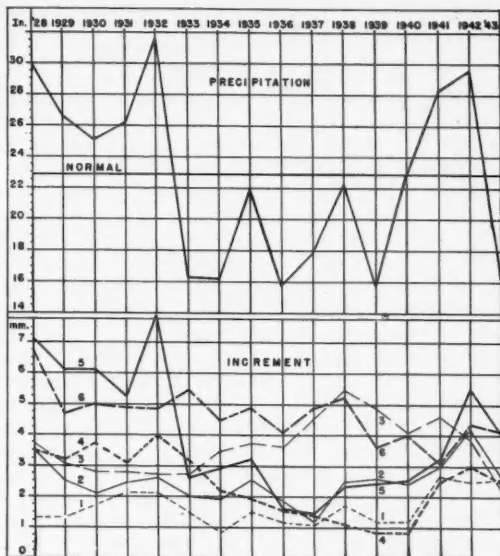


FIG. 62. (UPPER) Graphs showing the annual precipitation with departure from the normal at Hays, Kansas, before, during, and following the great drought. (LOWER) Graphs showing average annual increments of growth of hackberry and American elm in dry habitats (1 and 4), intermediate ones (2 and 5), and in wet sites (3 and 6).

STUDIES ON HACKBERRY

Studies on hackberry were made in dry ravines at three widely separated stations. These were in a pasture at Hays, at Hill City 50 miles northwest of Hays, and near Plainville 16 miles north of Hays. The trees were 30 to 45 years old, 6 to 17 inches in diameter (measured as were all the trees, at 3 feet in height), and 16 to 20 feet tall. The millimeters of increase in growth during the wet and dry years were 14.7 and 11.5, 25.5 and 14.5, and 11.4 and 10.4, respectively.⁴ The last ravine was an extremely dry one, which accounts for the slow growth. Great differences were found here in the growth of different trees. The average increment of growth during the wet years was 17.2 mm. It was 29 percent less during the dry years (12.2 mm.).

The first station with an intermediate habitat was 12 miles southeast of Hays at Munjor on Big Creek. The second was at Hill City near Jack Creek, and the third 16 miles north of Hays at Stockton. The trees were 43 to 64 years old, 9 to 17 inches in diameter, and 20 to 30 feet high. Millimeters of increase in radius during wet and dry periods were 23.0 and 17.1, 27.7 and 27.1, and 27.9 and 20.2, respectively. The average increment of growth during the wet years was 26.2 mm. It was 18 percent less during the dry ones (21.5 mm.).

Since trees were far more abundant in wet habitats along continuously flowing streams where the water

⁴ Foresters ordinarily give similar growth data in inches of increase in diameter at breast height (4.5 feet above ground)—the commonly accepted height for such measurements.—C. F. K.

table was high, larger numbers of samples were taken. Cores were obtained on Big Creek near Hays, on Walnut Creek near Rush Center 30 miles southward, and on Sawlog Creek 80 miles southwest of Hays. These trees were 26 to 100 years old, 8 to 23 inches in diameter, and from 25 to 60 feet tall. The millimeters of radial growth during the wet period and the dry one were 27.5 and 30.5, 17.0 and 18.5, and 15.2 and 13.3, respectively. The average growth increments for the two periods were 19.9 and 20.8 millimeters, respectively. Thus, growth was slightly greater here during the dry years.

During the wet years rate of growth was 66 percent as great in the dry habitats and 76 percent as much in the wet ones as that in the intermediate sites. Similar values during the dry years were 57 and 97 percent.

STUDIES ON AMERICAN ELM

Cores were obtained from elms growing in three different sites as described for hackberry, except a dry ravine 40 miles north of Hays at Stockton was substituted for the one at Hill City, since no elms grew there. These trees were 27 to 48 years old, 5 to 18 inches in diameter, but only 16 to 30 feet tall. The increments of growth in millimeters during the dry and wet years were, in the same order as for hackberry, 23.8 and 14.7, 22.5 and 12.5, and 16.8 and 13.2. Great variation occurred at the second station. One tree, apparently much more favorably and deeply rooted in the rock crevices than the others, made growth increments of 35 and 23 mm., while for another, some rods distant, they were 7.5 and 6.9. In one tree growth during drought even slightly exceeded that during the wet years. The average increments of growth of all trees during the wet years was 21.0 mm. It was 35 percent less (13.5 mm.) during drought.

Trees in two intermediate habitats were sampled. One was the first such habitat where hackberry also grew; the other was 40 miles northeast of Hays near Natoma. The trees were 54 to 70 years old, 9 to 25 inches in diameter, and 30 to 40 feet tall. Growth increments in millimeters in the usual sequence were 43.4 and 20.2, and 16.1 and 16.5, respectively. Averages were 29.8 and 18.4.

Cores were obtained from elms at five stations in wet habitats. The first three were those named as wet habitats for hackberry. Another was near a marsh on the Smoky Hill River near Hays, and the fifth was on the Saline River near Plainville, 16 miles north of Hays. The trees were 20 to 66 years old, 9 to 22 inches in diameter, and 25 to 50 feet high. Growth increments in millimeters at the several stations were, in order, 37.5 and 36.6, 37.1 and 37.3, 24.8 and 29.9, 37.0 and 46.0, and 46.3 and 38.9. The average increments of growth for all trees during the wet years was 36.5 millimeters and for the dry ones 37.7. During both wet and dry years growth of elm was most rapid in the wet habitats. During wet years it was 18 percent less in intermediate habitats and 42 percent less in dry ones. Similar decreases for

TABLE 11. Average increment of growth of hackberry and American elm at each of several sites in dry, intermediate, and wet habitats during a period of eight wet years (W) and a similar period of drought (D). Average age and size of the trees are also given.

Habitat	HACKBERRY			
	Growth	Age	Diam.	Height
	<i>mm.</i>	<i>years</i>	<i>inches</i>	<i>feet</i>
Hays.....	W 14.7			
Ravine.....	D 11.5	36	8	19
Hill City.....	W 25.5			
Ravine.....	D 14.5	38	13	19
Plainville.....	W 11.4			
Ravine.....	D 10.4	38	7	16
Mean average.....	W 17.2 D 12.2	37	9	18
Munjoy.....	W 23.0			
Big Creek.....	D 17.1	53	13	23
Hill City.....	W 27.7			
Jack Creek.....	D 27.1	48	13	22
Stockton.....	W 27.9			
Dry wash.....	D 20.2	53	12	30
Mean average.....	W 26.2 D 21.5	51	13	25
Hays.....	W 27.5			
Big Creek.....	D 30.5	49	9	42
Rush Center.....	W 17.0			
Walnut Creek.....	D 18.5	57	15	36
Jetmore.....	W 15.2			
Sawlog Creek.....	D 13.3	55	14	28
Mean average.....	W 19.9 D 20.8	54	13	35

Habitat	AMERICAN ELM			
	Growth	Age	Diam.	Height
	<i>mm.</i>	<i>years</i>	<i>inches</i>	<i>feet</i>
Hays.....	W 23.8			
Ravine.....	D 14.7	40	11	21
Stockton.....	W 22.5			
Dry wash.....	D 12.5	36	7	17
Plainville.....	W 16.8			
Ravine.....	D 13.2	48	18	29
Mean average.....	W 21.0 D 13.5	41	12	22
Munjoy.....	W 43.4			
Big Creek.....	D 20.2	58	25	30
Natoma.....	W 16.1			
Dry wash.....	D 15.5	60	12	37
Mean average.....	W 29.8 D 15.4	59	18	33
Hays.....	W 37.5			
Big Creek.....	D 36.6	45	19	43
Rush Center.....	W 37.1			
Walnut Creek.....	D 37.3	40	16	32
Jetmore.....	W 24.8			
Sawlog Creek.....	D 29.9	53	18	33
Hays.....	W 37.0			
Smoky Hill River.....	D 45.0	20	15	22
Plainville.....	W 46.3			
Saline River.....	D 38.9	27	12	39
Mean average.....	W 36.5 D 37.7	37	16	34

the dry years were 51 and 64 percent. These data are summarized in Table 11.

EFFECTS OF DROUGHT ON ANNUAL INCREMENT

The effect of drought upon radial growth may be more plainly seen where the yearly growth increments (1928 to 1943) are shown by graphs. Both hackberry and elm were sampled in dry, intermediate, and wet habitats at Hays and the data are shown in Figure 62. It is significant that in the dry habitat from 1928 to 1934 the increment in the elm (Graph 4) was about twice that of the hackberry (Graph 1). Then the growth rate of elm decreased, until in 1938 it was less than that of hackberry, and except for one year (1942) it remained less.

Growth of both species in intermediate habitats (Graphs 2 and 5) corresponded well with the graph of precipitation. Fluctuations in the growth of elm were very much greater than those of hackberry. Also the rate of growth was much higher until the beginning of drought in 1933. But during the drought, rate of growth was much the same in both species. With the return of abundant soil moisture the elm again grew more rapidly.

In wet habitats the growth increment in the elm (Graph 6) was again nearly twice that of the hackberry (Graph 3) during the wet period previous to the drought. Furthermore, no great decrease occurred during drought in either species. In fact, the trend generally was upward in the hackberry until near the end of the drought. From 1938 until 1941 the increment was even slightly greater in the hackberry than in the elm. The general trend in both species, however, was downward after 1938, except that growth in elm increased when soil moisture became plentiful.

These graphs indicate that elm was more adversely affected by drought than hackberry, and also that it grew more rapidly in intermediate habitats except during drought than in either dry or wet ones. Moreover, rate of growth of hackberry in wet habitats was greater during drought than during the wetter years. Elm also grew quite as well in wet places during the dry years as before or following them.

In the study of these and the following species of trees only general correlations with growth in dry, intermediate, and wet sites during periods of high and low precipitation have been pointed out. Irregularities in growth may have been due in part to reduced or increased vigor following drought, to eccentric growth which would result in errors in the samples, or to damage to the foliage by insects or fungi or by wind and high temperatures. Twigs and branches may have been damaged directly by high insolation when foliage became sparse or by effects produced by scorched leaves which remained attached to them (Reed & Bartholomew 1930). Degree of lowering of the water table and poor aeration of soil during rainy periods are, of course, factors of the environment. While these were not measured, nor variation due to other possible causes studied, yet it seems clear that the chief cause of periodic variation in growth was due overwhelmingly to the

changing environment and much less to any other cause or combination of causes.

STUDIES ON ASH

Samples were taken from trees in a timber claim on level upland near Goodland in northwestern Kansas. The planted area was originally about 20 acres. A cultivated field on the west had been the source of much dust which had blown into the grove and buried the trunks of some trees to a depth of 2 to 4 feet. The north end of the long rectangular grove was bounded by a deep ditch along the highway. This supplied extra water for growth and was actually a moderately moist site. Except here, drought had taken so heavy a toll that only a few living trees remained. These were along the north end of the west border and between this border, and the trees along the road. All the trees had been injured by drought, especially in the tops of the crowns, but dead branches also occurred near the base. Replacement of branches from dormant buds on living trees gave grotesque shapes to these relicts. Cores were taken only from those individuals least damaged; some from those on the western edge and others from the interior. These trees, which average 28 years in age and 5 inches in diameter, were only 17 feet tall. That the increment of growth was very small is shown in Table 12.

The trees near the ditch which were older and much larger were used as an example of an intermediate habitat. Here growth was more than twice as great as in the dry sites during the dry years and also much greater during the wet ones. Cores of ash in intermediate sites were taken at three other stations where hackberry or elm or both had been sampled. The average increment of growth during the wet years was 26.8 mm. or 77 percent greater than that in the dry sites (15.1 mm.). During the dry years the increment was only 16.7 mm., but even this was more than 2.5 times greater than that in the dry sites (6.0 mm.).

Cores from trees in wet habitats were taken along creeks or rivers at Hays, Rush Center, Jetmore, Plainville, and Hill City, where previous work had been done. In addition samples were also taken on Sappa Creek about 5 miles north of Edson, which is east of Goodland. The results are shown in Table 12, where it may be seen that the average rates of growth during the wet and dry years were only slightly different (28.0 mm. and 26.3 mm., respectively). Nor did this much exceed average growth in the intermediate habitats during wet years. But during drought it was 57 percent greater. The slowest growth occurred at Jetmore, the most southwesterly station and consequently the most arid one.

RELATIVE GROWTH OF HACKBERRY, ELM, AND ASH

Growth of the three species of forest trees in each of the three habitats may be understood better by examination of Table 13. Data on ash from the dry habitat are not included since only at Goodland had the trees been transplanted. Increment in elm growing in dry habitats was greater than it was in hackberry.

TABLE 12. Average increment of growth of green ash and cottonwood at each of the several sites in dry, intermediate, and wet habitats during a period of eight wet years (W) and a similar period of drought (D). Average age and size of trees are also given.

Habitat	GREEN ASH			
	Growth	Age	Diam.	Height
	mm.	years	inches	feet
Goodland.....	W 11.8			
Edge of grove.....	D 7.1	28	5	16
Goodland.....	W 18.4			
Interior of grove.....	D 4.9	28	5	17
Mean average.....	W 15.1 D 6.0	28	5	17
Goodland.....	W 23.1			
Grove near ditch.....	D 14.8	43	10	24
Hill City.....	W 29.9			
Jack Creek.....	D 16.4	20	6	20
Munjoy.....	W 32.0			
Big Creek.....	D 25.1	44	16	30
Natoma.....	W 22.3			
Dry wash.....	D 10.6	52	10	33
Mean average.....	W 26.8 D 16.7	40	11	27
Hays.....	W 32.8			
Big Creek.....	D 40.3	28	11	41
Rush Center.....	W 32.6			
Walnut Creek.....	D 32.0	45	15	38
Jetmore.....	W 14.7			
Sawlog Creek.....	D 13.0	53	9	28
Plainville.....	W 23.9			
Saline River.....	D 25.1	37	11	38
Hill City.....	W 36.8			
Jack Creek.....	D 27.7	20	8	22
Edson.....	W 27.4			
Sappa Creek.....	D 19.6	23	8	27
Mean average.....	W 28.0 D 26.3	34	10	32

Habitat	COTTONWOOD			
	Growth	Age	Diam.	Height
	mm.	years	inches	feet
Syracuse.....	W 8.5			
Dry wash.....	D 9.5	65	24	40
Brownell.....	W 39.5			
Grove.....	D 29.0	22	12	30
Wakeeney.....	W 29.0			
Dry wash.....	D 16.9	65	36	60
Hill City.....	W 22.9			
Hedgerow.....	D 14.1	51	16	36
Mean average.....	W 25.0 D 17.4	51	22	42
Hays.....	W 37.0			
Smoky Hill River.....	D 30.0	35	24	40
Hays.....	W 64.5			
Dry wash.....	D 36.5	30	23	38
Hill City.....	W 52.1			
Jack Creek.....	D 27.9	26	19	39
Hill City.....	W 82.8			
Springs, Jack Creek.....	D 55.0	35	27	45
Mean average.....	W 59.1 D 37.4	32	23	41
Hays.....	W 61.5			
A marsh.....	D 87.0	20	14	30
Rush Center.....	W 39.8			
Walnut Creek.....	D 53.8	65	22	40
Mean average.....	W 50.7 D 70.4	43	18	35

TABLE 13. Average total growth in mm. of hackberry, elm, and ash during eight wet years (W) and eight dry ones (D), in dry, intermediate, and wet habitats.

Habitat	Hackberry		Elm		Ash	
	W	D	W	D	W	D
Dry.....	17.2	12.2	21.0	13.5
Intermediate.....	26.2	21.5	29.8	18.4	26.8	16.7
Wet.....	19.9	20.8	36.5	37.7	28.0	25.3

In the intermediate habitats elm again grew more rapidly than the other species during the wet years, but was exceeded in rate of growth by hackberry during the dry ones. Ash grew at the same rate as hackberry during the wet period, but was exceeded by both hackberry and elm during the dry period.

Elm made its best growth during both wet and dry periods in the wet habitats. Ash grew much more rapidly here than in the intermediate site during the dry period, and slightly better during the wet one. But hackberry made its most rapid growth in the intermediate habitats. In the wet habitat the growth of elm was most rapid, and that of hackberry the slowest.

STUDIES ON COTTONWOOD

Rate of growth of cottonwood was studied at Syracuse near the Kansas-Colorado state line in the drier southwestern part of Kansas, at Brownell 45 miles southwest of Hays, as well as at Wakeeney northwest of Hays, and at Hill City. Growth was very slow at Syracuse, and averaged slightly better during the dry years than the wet ones. Mean average growth in the dry sites was 25.0 mm. during the period of wet years, and 17.4, or 30 percent less, during the dry ones (Table 12).

At the four stations representing intermediate habitats, growth was 59.1 mm. during the 8 wet years and 37.4 during drought.

The growth increment was higher in the wet habitat at Rush Center during the dry years and very much higher at Hays than during the wet ones. Mean average increment was 50.7 mm. in wet years but 70.4 in drought. Thus, growth during dry years was 53 percent less in dry habitats than in intermediate ones, and in wet habitats 88 percent greater. But during wet years growth was 58 percent less in dry habitats and 14 percent less in wet ones than in intermediate sites. Cottonwood grew much faster in all habitats than hackberry, elm, or ash.

STUDIES ON BUR OAK AND OSAGE ORANGE

Rate of growth of bur oak was ascertained in an intermediate site at Natoma and a wet one on Salt Creek near Paradise, 40 miles northeast of Hays. During wet and dry periods, respectively, growth in the moderately moist site was 17.1 and 10.8 mm. At both stations the trees averaged 54 years in age; they were 12 to 15 inches in diameter but only 36 to 38 feet tall. Increase in radius during the wet years in the wet habitat (18.6 mm.) was scarcely greater

than that in the drier ones. But during the dry period the trees grew more rapidly (14.4 mm.) than those in the intermediate site.

Effects of wet and dry periods on the growth of Osage orange were ascertained for a number of trees in a timber claim on upland (dry site) and where they extended across a ravine (intermediate site) near Kush Center. In the dry site trees 5 inches in diameter, 10 feet high, but 38 years old grew 15.2 mm. and 10.2 mm. during wet and dry periods, respectively. Trees in the ravine were 9 inches in diameter, 15 feet high, but only 30 years old. Their growth rate during wet years (22.6 mm.) and dry ones (20.1 mm.) was 33 and 49 percent greater, respectively, than that in the same timber claim on the upland.

SUMMARY

This study describes the effects of the greatest drought since the beginning of recorded weather history on forests and trees growing in a prairie climate. The area considered extends from central Iowa westward into Colorado and includes the territory from southern Oklahoma to Canada.

Data are from a wide range of sources; they include predrought surveys of trees and conditions for their growth in grassland which give a necessary background for an understanding of their injury and death or recovery in different sites. The most intensive studies were made in the western half of Kansas.

A major area of postclimax forest occurs along the Missouri River. Here the forests are composed of several communities; red oak-linden (*Quercus borealis maxima-Tilia americana*) is the most mesic, black oak-shagbark hickory (*Quercus velutina-Carya ovata*) is intermediate, and bur oak-bitternut hickory (*Quercus macrocarpa-Carya cordiformis*) the most xeric. Communities of shrubs often occur as a transition from forest to prairie. In Nebraska all of these forests suffered heavily from drought as they did elsewhere, at least when pastured.

Decrease in size of individuals, decrease in number of species, and confinement to the most protected sites are marked northward, and especially westward where the climate becomes more arid. A height of trees of 70 to 90 feet diminishes rapidly to 25 to 45 feet; rate of growth in diameter decreases one-half or more 150 miles westward from the Missouri River.

Along prairie streams westward from the Missouri River forest communities rapidly disappear, and the typical condition is an intermingling of forest trees along the flood plain. Farther westward trees are mostly confined to the banks of the larger streams and to broad, shallow ravines tributary to them, or to the vicinity of springs. Some are found in the shelter of steep protecting bluffs. In the driest prairies trees occur naturally, if at all, only as small groups or as individuals in the most protected places along streams. Planted trees occur in timber claims, windbreaks, and hedgerows, but sparsely in the more arid western prairies.

Early effects of the drought were very impressive and widely reported; the literature revealed that in Minnesota 40 percent of all the trees in shelterbelts, mostly boxelder, willow, green ash, silver maple, and cottonwood, were considered dead or dying in 1934. In North Dakota practically all maturing cottonwoods, willows, and boxelders were killed, except where the water table was continuously high; the boxelders often recovered by root sprouts. Great damage to trees occurred in Montana. Losses by death of coniferous trees in Iowa in the spring of 1934 ranged from 5 to 39 percent. Trees in central Kansas showed 41 percent death or injury and those westward 55 percent in 1936. In central Oklahoma 20 to 50 percent death of trees occurred and much higher losses of 35 to 79 percent were reported in western Oklahoma by 1937. Reconnaissance of tree plantations late in 1934 showed 43 percent survival of standing trees in North Dakota, 32 in South Dakota, 18 in Nebraska, and 28 in the Oklahoma-(northern) Texas area. As the drought progressed earlier losses were greatly increased.

Predrought data on mean annual precipitation, average weekly evaporation, and water content of soil from eastern Nebraska, north-central Kansas, and eastern Colorado are presented. They show clearly the semiarid environment west of the Missouri River and why it becomes even more inimical to growth of trees westward. A period of dry years preceded the severe drought. Precipitation was lowest in 1934 and 1936, but because of previous desiccation of soil and vegetation 1939 was also one of the worst drought years. The extremely low precipitation during these years and the weekly amounts of available soil moisture (which were very frequently nil to 6 feet in depth during the drought) were ascertained. The water table in many ravines and lowland terraces fell 3 to 4 or more feet over much of the Midwest. Trees on upland root far above the normal water table. Evaporation was extremely high and sometimes one-third or more greater than during a predrought year. Increases of 6° to 15° F. in average weekly temperatures were common, and average weekly maximum temperatures of 101° to 109° sometimes occurred.

The chief cause of injury was a lack of sufficient available water. This was due to low precipitation but was accentuated by one or more of several causes, as competition for water by grasses, decreased rate of water infiltration and rapid runoff, drying up of streams and springs, and a rapid fall of the water table in ravines and lowland terraces. Lack of an adequate water supply also resulted from low humidity, high evaporation, desiccating winds, and the inability of trees to accommodate their root systems to the rapidly changing environment. Unrestricted grazing was a common cause of excessive mortality in timber claims and windbreaks.

Experimental data on the harmful effects of competition with grass on both roots and shoots of trees have been presented. Root distribution of the same tree species in different types of soil including alluvial soil with a high water table has been noted, and the

general relation between root extent and distribution in different sites to drought resistance is pointed out.

Injury and death of woody plants due to the effects of drought were often the results of continuous adverse conditions over an extended period of time. But death of trees and shrubs on flood plains and terraces sometimes occurred in a relatively short time if the water table lowered rapidly. Effects of early drought were wilting, discoloring, withering, or shedding of the foliage. An early outward sign of repeated yearly drought among deciduous trees was great reduction in size and number of leaves and defoliation of the outer portions of the crown. Great injury was also often caused by partial or total and sometimes repeated defoliation by grasshoppers, web worms, and leaf-eating larvae of other insects; such attacks usually occurred during the years of great drought.

Exposure of branches with reduced foliage to high insolation, great heat, and low humidity was a common cause of injury. Desiccation resulted in the death of the smaller branches, and permitted the entrance of wood borers, other insect larvae, and fungi. Desiccation and wood borers caused the death of the branches to proceed rapidly downward; often the entire tree succumbed.

In western Kansas, which is representative of other prairie states in this latitude, counts on hundreds of trees were made in 1935 and again late in the drought or after its close. Losses in the most xeric places where trees grew naturally were high, in dry ravines (American elm (*Ulmus americana*) 70 percent, and hackberry (*Celtis occidentalis*) 36) and on bluffs (American elm 56, hackberry 28, and green ash (*Fraxinus pennsylvanica lanceolata*) 33 percent). Losses of red cedar (*Juniperus virginiana*) were usually less than any of the preceding. Average losses in percentage of trees along continuously flowing streams and intermittent streams were American elm 5 and 62, hackberry 5 and 75, and cottonwood (*Populus sargentii*) 6 and 59. Loss of willows (*Salix* spp.) along intermittent streams was 70 percent. Death of trees growing near running springs was rare. But about springs that almost failed to flow in drought, a mortality of 55 percent of cottonwoods and 89 percent of willows was recorded.

Destruction in long-established timber claims was high. Severe losses occurred during dry periods previous to 1933; the great drought almost annihilated the survivors. Where 45 percent of Osage orange and 86 percent of green ash were dead in 1935, all had succumbed by 1939. Even in tree claims on lowland early in drought black locust (*Robinia pseudoacacia*) had lost 75 percent and cottonwood 14 percent.

Losses of trees in windbreaks were nearly always heavy. Dust storms contributed greatly to this loss through partial burial of the trees in great drifts of soil, sometimes 4 to 8 feet deep. Losses of green ash, American elm, hackberry, and other deciduous trees were frequently 80 to 90 percent and sometimes

maore. In some places trees of red cedar alone survived.

Of 3,200 trees in a hedgerow of Osage orange (*Maclura pomifera*) all but 15 succumbed. Such high losses were typical.

Average losses of trees in Nebraska and Kansas were probably 50 to 60 percent by death and an additional 20 to 25 percent suffered severe to moderate injury. Red cedar, hackberry, and bur oak endured drought especially well; silver maple, boxelder, and cottonwood seemed less well adapted to endure long-continued drought.

Effect of drought upon the radial growth of uninjured or least injured trees in western Kansas was ascertained. Cores were taken with an increment borer from 3 to 8 trees of hackberry and American elm in each of three sites (dry, intermediate and wet) at each of 3 to 5 widely separated stations in western Kansas. Growth during 8 good years was compared with that during 8 dry ones. During the good years rate of growth of hackberry was 66 percent as great in the dry habitats and 76 percent as much in the wet ones, as that in the intermediate sites. Similar values during the dry years were 57 and 97 percent. During both good and dry years growth of elm was most rapid in the wet habitats. During good years it was 18 percent less in intermediate habitats and 42 percent less in the dry ones. Similar decreases for the dry years were 51 and 64 percent.

In dry habitats from 1928 to 1934, the increment of growth in American elm each year was about twice that of hackberry. Then its growth rate decreased until in 1938 it was less than that of hackberry, and remained less even after the drought. In intermediate habitats fluctuations of growth in elm were much greater than those in hackberry. In wet habitats the general trend of hackberry was upward until near the end of the drought, but growth rate of elm decreased slightly.

Average rate of growth of green ash was about the same in both wet and intermediate habitats on good years, but in dry habitats it was only slightly more than half as great. But on dry years the average rate of growth decreased 36 percent in intermediate habitats from that in wet ones and 77 percent in the dry habitats. Ash in intermediate habitats during the wet period grew at the same rate as hackberry, but less rapidly than elm; but in wet habitats during the dry period it grew more rapidly than hackberry but less rapidly than elm. Rate of growth of cottonwood, bur oak, and Osage orange were also determined.

Trees that retained some life at the close of the drought usually remained alive temporarily unless infestation by wood borers was so complete or the trees so nearly dead that they were unable to resume growth. Recovery was shown principally and commonly by renewed growth locally within the crown. In dry sites even after 3 or 4 years of good precipitation leafy branches were sometimes few and foliage was sparse. But where drought had been less severe

foliage of the renewed portions of the crown was unusually dense. Often the dead branches in the tops of the crown were soon obscured by new ones where moisture was plentiful. Sprouts developed from the bases of certain trees grew rapidly. Dead trees were partly replaced by seedlings but only where the trees grew naturally. In this manner red cedars continued to replace their losses throughout the drought. Seedlings were not found in timber claims, windbreaks, or hedgerows in mixed prairie, and only rarely in unpastured places eastward to the Missouri River.

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LIMNOLOGICAL STUDIES OF WESTERN LAKE ERIE

V. RELATION OF LIMNOLOGICAL AND METEOROLOGICAL CONDITIONS TO THE PRODUCTION OF
PHYTOPLANKTON IN 1942

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LIMNOLOGICAL STUDIES OF WESTERN LAKE ERIE

INTRODUCTION

Phytoplankton occupies a basic position in the trophic cycle of a lake; therefore, the size of the annual crop of these primary producers directly or indirectly affects the welfare of all the consumers in the lake. After four and one-half years of continuous observation of western Lake Erie it has become apparent that each year is different in respect to the quality and the quantity of phytoplankton and the nature of the physical and chemical conditions that affects this plankton. General statements concerning phytoplankton production in these waters based on observations limited to a season or even a complete year might be very misleading. It is quite likely that this condition is not peculiar to western Lake Erie. The importance of year-round observations is emphasized throughout this report since it is believed that such an approach is the most effective means of acquiring basic information on lake production.

In these studies on the annual production of phytoplankton in western Lake Erie an attempt is made to evaluate the factors responsible for annual variations. Some of these factors have been under continuous measurement since these studies were begun, and each year as circumstances permit new ones are added. This report, the fifth in the series, presents results of observations made during 1942. In addition to the consideration of the same factors observed in previous years, this report also includes data on ammonia, nitrite, and nitrate nitrogen, and total and dissolved phosphorus. The junior author is largely responsible for these additions.

The writers wish to express their appreciation to the U. S. Geological Survey offices in Lansing, Michigan, and Columbus, Ohio, for data on river discharge and run-off; to the Division Filtration Plant in Cleveland, Ohio, for data on daily plankton counts and daily turbidity readings; to the Collins Park Filtration Plant in Toledo, Ohio, for daily turbidity readings; to the U. S. Lake Survey Office in Detroit, Michigan, for the graph showing the seiche of January, 1942, and for data on daily mean lake levels at Cleveland, Ohio; and to various members of our laboratory staff for general assistance.

PHYSICAL CONDITIONS

TEMPERATURE

Water and air temperatures, based on weekly means, are shown in Figure 1 B. The marked similarity between these curves, except when the lake was covered with ice, reflects the shallowness of the lake. Air temperatures at Put-in-Bay ranged from a minimum daily mean of 0.6°C . to a maximum daily mean of 29.7°C .; the annual mean was 10.1°C . Maximum and minimum daily means and the annual

mean were lower in 1942 than in 1941. Throughout the year daily water temperatures did not vary more than 2.0°C . from the surface to bottom except on a few occasions in spring and early summer. These exceptions were associated with calm warm days which resulted in a rapid warming of the surface water. Only on these occasions was the vertical temperature gradient sufficient to be classified as a thermocline. The minimum daily mean water temperature of 0.3°C . existed during most of January and February, and part of December, at which time an ice cover was present. A maximum daily mean of 26.4°C . occurred on July 21. In 1941 the maximum daily mean and the annual mean water temperatures were both higher than in 1942.

The following discussion of heat budgets and the amount of heat stored in the lake water for each week in the year is based on calculations using weekly mean temperatures and weekly mean depths. Weekly means were derived from daily means and the calendar year was divided into 52 weeks with the first day of January being the first day of the first week. If the annual heat budget of this lake were calculated on the basis of daily mean temperatures rather than weekly means it would be about 7.3 percent higher. The latter method is used in this paper because data pertaining to other factors are reduced to weekly mean values whenever possible. The fact that the water level of Lake Erie may vary appreciably with season and year necessitates frequent corrections for mean depth. The mean depth of this part of the lake, as determined by a planimeter, was found to be 7.5 m. for low water datum. Navigation charts of Lake Erie, from which the mean depth was determined, are constructed on the basis of low water datum, which is 570.5 ft. above mean tide at New York. In 1942 corrections for mean depths were made on the basis of the difference between the low water datum and the mean lake level for each week. Variations in the weekly mean depths are shown in Table 1.

Corrections for weekly mean depths were not applied in calculating the heat budgets of 1940 and 1941, since complete data on daily lake levels were not available at that time. The mean depth used in calculating the 1941 annual heat budget was 7.5 m., but the actual mean depth at the time of the maximum summer temperature was 7.9 m. When this correction is applied the 1941 annual heat budget becomes 20,382 g-cal. per cm^2 instead of 19,575 as previously stated (Chandler 1944). This correction increases the annual heat budget by 4.1 percent. In this paper when comparisons are made between the years 1941 and 1942, in respect to annual heat budgets, amount of heat stored, and the rate of gain or loss of this heat they are based on calculations corrected for variations in mean depth.

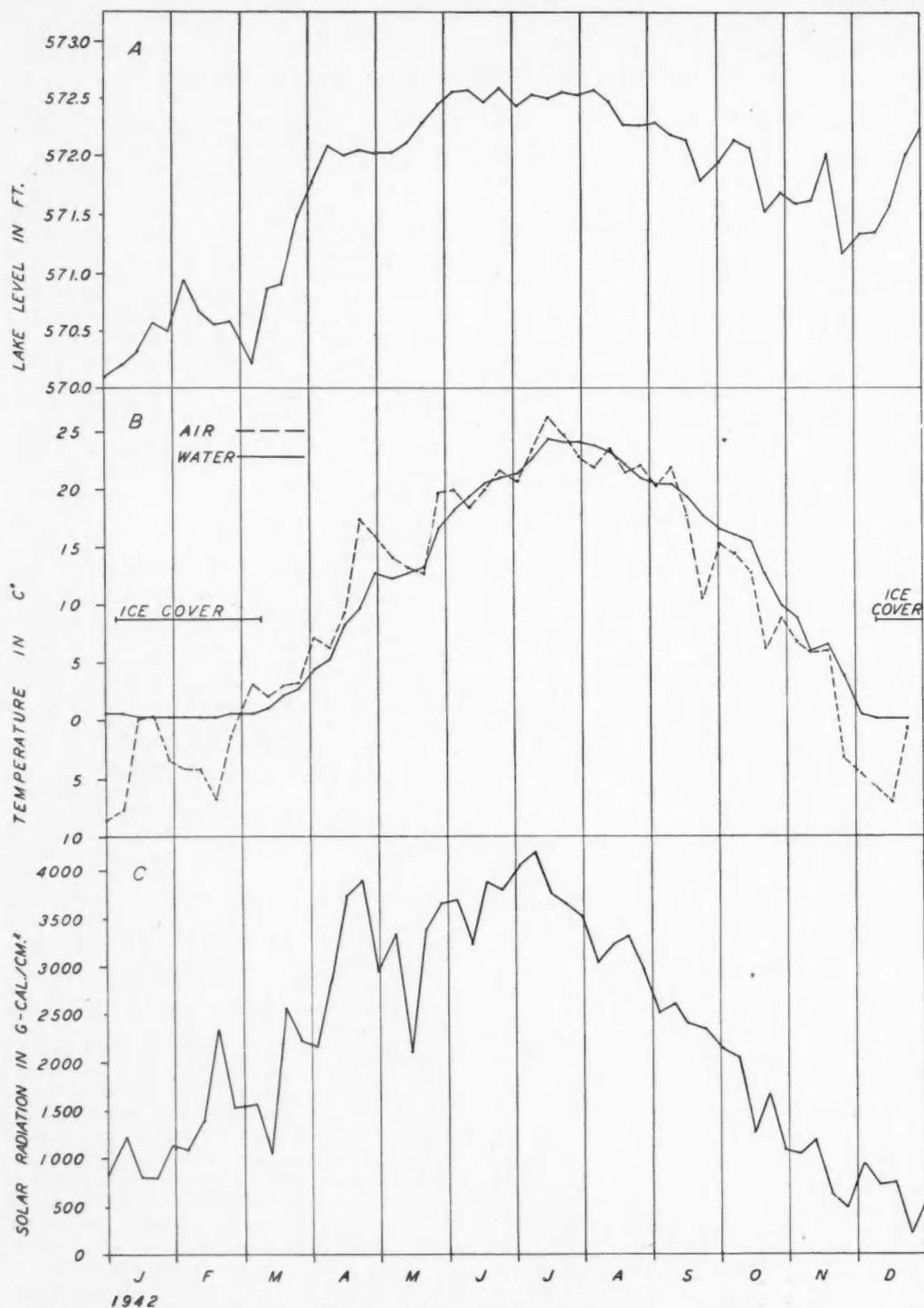


FIG. 1. A. Weekly mean lake levels, in feet, at Put-in-Bay. B. Weekly mean air and water temperatures, and the period of ice cover on the lake, at Put-in-Bay. C. Total weekly amounts of solar and sky radiation at Put-in-Bay.

In 1942 the annual heat budget was 19,764 g-cal. per cm.² which is 3.0 percent less than that of 1941. The weekly mean water temperature was 0.6° C. at the time the ice cover formed on January 5, and also when it disappeared on March 9. The weekly mean depths were 7.4 m. for both of these dates. By definition then the winter heat budget was 0.0. Daily fluctuations in water temperature did occur during the period of ice cover, but most of the time it was about 0.3 C. Likewise, the mean depth varied dur-

TABLE 1. Amount of heat stored in the lake water (weekly mean temperature x mean depth) and weekly gain or loss of heat, 1942.

Week beginning (1942)	Weekly mean temp. °C.	Mean depth m.	Heat stored g-cal./cm. ²	Gain (+) or loss (-) over preceding week
Jan. 1.....	0.6	7.4	444	- 456
8.....	0.6	7.4	444	0
15.....	0.3	7.5	225	- 219
22.....	0.3	7.5	225	0
29.....	0.3	7.5	225	0
Feb. 5.....	0.3	7.6	228	+ 3
12.....	0.3	7.6	228	0
19.....	0.3	7.5	225	- 3
26.....	0.6	7.5	450	+ 225
Mar. 5.....	0.6	7.4	444	- 6
12.....	1.1	7.6	836	+ 392
19.....	2.2	7.6	1,672	+ 836
26.....	2.8	7.8	2,184	+ 512
Apr. 2.....	4.7	7.9	3,713	+1,529
9.....	5.3	8.0	4,240	+ 527
16.....	8.3	8.0	6,640	+2,400
23.....	9.7	8.0	7,760	+1,120
30.....	12.8	8.0	10,240	+2,480
May 7.....	12.3	8.0	9,840	- 400
14.....	12.8	8.0	10,240	+ 400
21.....	13.3	8.0	10,640	+ 400
28.....	16.7	8.1	13,527	+2,887
June 4.....	18.3	8.1	14,823	+1,296
11.....	19.4	8.1	15,714	+ 891
18.....	20.6	8.1	16,686	+ 972
25.....	21.1	8.1	17,091	+ 405
July 2.....	21.4	8.1	17,334	+ 243
9.....	22.8	8.1	18,468	+1,134
16.....	24.7	8.1	20,007	+1,539
23.....	24.4	8.1	19,764	- 243
30.....	24.4	8.1	19,764	0
Aug. 6.....	24.1	8.1	19,521	- 243
13.....	23.3	8.1	18,873	- 648
20.....	22.2	8.0	17,760	-1,113
27.....	21.1	8.0	16,880	- 880
Sept. 3.....	20.6	8.1	16,686	- 194
10.....	20.6	8.0	16,648	- 38
17.....	19.4	8.0	15,520	-1,128
24.....	17.8	7.9	14,062	-1,458
Oct. 1.....	16.7	7.9	13,193	- 869
8.....	16.1	8.0	12,880	- 313
15.....	15.6	7.9	12,324	- 556
22.....	12.8	7.8	9,984	-2,340
29.....	10.0	7.9	7,900	-2,084
Nov. 5.....	8.9	7.8	6,942	- 958
12.....	6.1	7.8	4,758	-2,184
19.....	6.7	7.9	5,293	+ 535
26.....	3.9	7.7	3,003	-2,290
Dec. 3.....	0.6	7.8	468	-2,535
10.....	0.3	7.8	234	- 234
17.....	0.3	7.8	234	0
24.....	0.3	8.0	240	+ 6

ing this period (Table 1). Winter heat budgets of western Lake Erie have not exceeded 1,200 g-cal. per cm.² since 1938, but only the 1942 budget was 0.0. The main sources of heat for the winter budget according to Juday (1940) are solar radiation, bottom muds, and drainage waters. Temperatures of bottom muds have not been investigated in this lake but the other two sources have been. In 1942 the total amount of solar radiation delivered to the surface of the lake, during the period of ice cover, was 6.0 percent less than that for the same period in 1941. The amount of tributary water entering this part of the lake during the same period was about 10.0 percent greater in 1942 than for the corresponding period in 1941. A large portion of this increase in 1942 was from the Raisin, Maumee, Portage, and Sandusky rivers. Waters from these rivers maintain a temperature only slightly above freezing during the winter months, since the source of water is run-off from cultivated areas. Thus during the period of ice cover in 1942, more cold water entered the lake than entered during 1941. This condition explains in part the absence of a winter heat income.

Acquisition of heat by the water subsequent to the disappearance of the ice cover resulted in a spring and summer heat budget of 19,764 g-cal. per cm.², which is the same as the annual heat budget, since the winter heat budget was 0.0. This spring and summer budget is equivalent to 33.6 percent of the total solar radiation delivered to the surface of the lake from the time of ice disappearance to the time of the maximum summer water temperature. In 1941 it was 31.6 percent. The annual heat budget in 1942 represented 16.8 percent of the total quantity of solar radiation delivered to this portion of the lake for the entire year; in 1941 the annual heat budget represented 15.0 percent of the total annual solar radiation.

In an attempt to describe the temperature cycle of western Lake Erie the amount of heat when water temperatures exceeded 0.0° C., present in a column of water having a height equal to the mean depth of the lake and a cross section area of 1 cm.², was determined for each week in the year (Table 1). This is referred to as the heat stored and is expressed in g-cal. per cm.² of lake surface. The value of this method is that the heat in the lake water is reduced to the same units as those used for measuring solar radiation, the ultimate source of heat for the lake. Table 1 also shows the amount of heat gained or lost over that of the preceding week.

The amount of heat present in the water from January to early March did not exceed 450 g-cal. per cm.² during any week. Variations were the least while an ice cover was present; this was due to the fact that a large amount of tributary water entered the lake at this time and also because neither wind nor solar radiation had direct contact with the water beneath the ice. Warming of the water began immediately with the disappearance of the ice cover and progressed with each week, except the week of May 7 (Table 1), until the annual maximum of 20,007 g-cal.

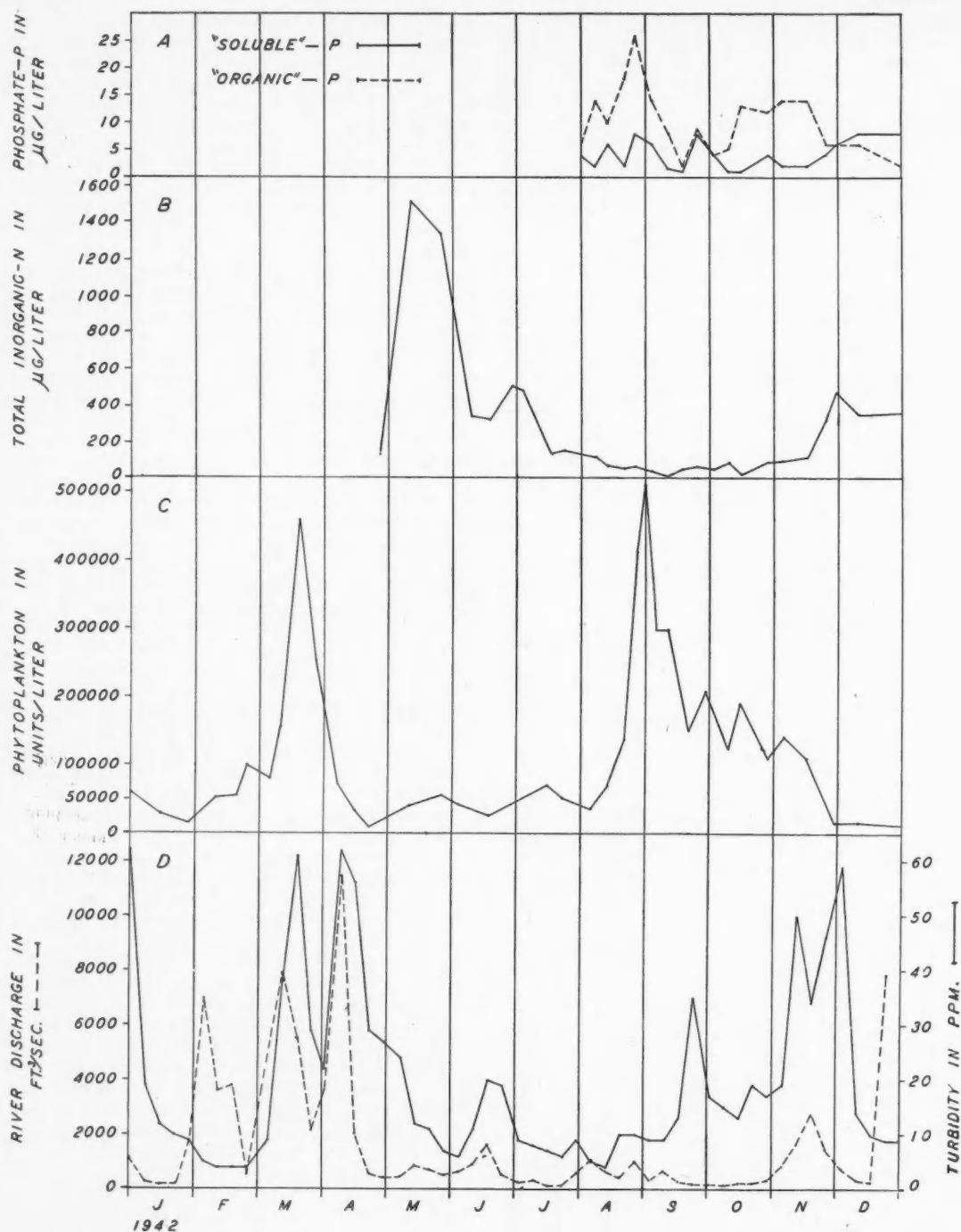


FIG. 2. A. "Soluble"-P and "organic"-P of the lake water. B. Total inorganic-N of the lake water. C. Total phytoplankton. D. The combined weekly mean discharge of the Raisin, Maumee, Portage, and Sandusky rivers, and the weekly mean lake turbidities at Put-in-Bay.

per cm.² was reached in mid-July. Rate of acquisition of this heat was slow or rapid depending upon the amount of solar radiation reaching the surface of the lake (Fig. 1 C), amount of water entering the lake through tributaries (Fig. 2 D), and the direction and velocity of wind. The number of lake level changes of 0.5 ft. or greater (Table 5) that occurred each week supply a rough index to wind conditions. The greatest amount of heat acquired by the water during any week was 2,844 g-cal. per cm.² on May 28, an amount equivalent to 78.8 percent of the total amount of solar radiation delivered to the surface of the lake. During the weeks of April 16 and 30, 2,400 and 2,480 g-cal. per cm.² respectively were gained; all other weekly gains were less than 1,600 g-cal. per cm.² In 1942 the water began to warm earlier than it did in 1941 and this may be attributed to the fact that the ice cover disappeared about three weeks earlier. Thus for corresponding weeks from early March to early April there was nearly twice as much heat stored in the water in 1942 as in 1941. But from April 9 to mid-July the weekly amounts of heat stored were less in 1942 than in 1941. Yet the 1941 annual heat budget was only 3.0 percent greater than in 1942.

The lake water began to lose heat in late July and this loss continued irregularly until late December (Table 1). Rate of cooling was greatest from late October to early December; this period was characterized by (1) strong winds which agitated and cooled the water, and (2) by reduced amounts of solar radiation (Fig. 1 C). The greatest weekly loss was 2,535 g-cal. per cm.² which occurred during the week of December 3; however, on four other occasions during autumn the weekly loss exceeded 2,000 g-cal. per cm.² (Table 1). The amount of heat stored in the lake water per week from late July to early October was a little greater in 1941 than in 1942, but from early October to December the situation was reversed. Late November and early December in 1942 were characterized by strong winds, low air temperatures, and snow. These conditions reduced the water temperature rapidly and an ice cover formed by mid-December, or about three weeks earlier than in the three previous years. It is apparent that in western Lake Erie the amount of heat present in the water at a given time varies widely from year to year, and the rate of gain or loss of this heat is controlled by prevailing meteorological conditions, especially air temperature, solar radiation, and wind. Church (1942) found a similar relationship between these conditions and the cooling of the water of Lake Michigan during the autumn of 1941. On account of its greater depth and volume, Lake Michigan has a lower annual maximum temperature and a higher annual minimum than does western Lake Erie, yet the rate of cooling in the two bodies of water appears to be quite similar.

ICE COVER

An ice cover formed in the island region on January 5 and remained intact until March 9. The lake

was frozen over also during most of December (Fig. 1 B). As in previous years it was difficult to determine how much of western Lake Erie was covered during this period. Available information indicates that more of the lake was free from ice in 1942 than in 1941; in 1942 open areas of water appeared irregularly a few miles distant from the islands. This suggests that the lake was open most of the winter except in the immediate vicinity of the islands. The spring break-up in 1942 was three weeks earlier than in either 1940 or 1941. This early break-up is reflected by the higher than usual water temperatures in mid-March. Ice attained a maximum thickness of 12 inches in late January; the average for the winter was about 8 inches. In addition to being thinner than usual the ice cover of 1942 was quite free from snow. The total snowfall for near-by Toledo during January, February, and March, 1942, was 12.6 inches, while the 57-year average is 20.2 inches (U. S. Weather Bureau, 1942).

SOLAR AND SKY RADIATION

The total amount of solar and sky radiation received at Put-in-Bay during 1942 was 117,492 g-cal. per cm.², which is about 7 percent less than that received in 1941. More solar radiation was received, however, during January, February, October, and December, 1942, than in the corresponding months of 1941. In comparison with 1941, the greatest deficiencies in 1942 were 2,418 g-cal. per cm.² in March and 3,825 in May. These differences are reflected in the differences in water temperatures during the spring months of the two years. Data published in the Monthly Weather Review (1942) show that Put-in-Bay received more solar radiation in 1942 than did other stations of similar latitude. The total amount of solar radiation, in g-cal. per cm.², received by six of these stations is as follows: Madison, Wisconsin, 115,643; Chicago, Illinois, 109,910; State College, Pennsylvania, 112,962; New York City, 111,149; and Blue Hill, Massachusetts, 114,388. Inspection of Figure 1 C, shows that the seasonal increase in solar radiation at Put-in-Bay began in early February and continued with many irregularities to the summer maximum in July. Following this maximum the weekly amounts decreased with regularity to the yearly minimum in December. The maximum weekly amount was 4,199 g-cal. per cm.² during the week of July 9, and the minimum was 229 during the week of December 24. The largest daily total amount received was 746 g-cal. per cm.² on May 10 and the smallest was 8 on December 30.

RIVER DISCHARGE

Western Lake Erie, comprising about 5 percent of the total volume of the entire lake, receives approximately 90 percent of all the drainage water entering the lake. The effects of this on the general limnological conditions in the western end are numerous, but among the more conspicuous are those related to temperatures, turbidities, lake levels, and nutrients essential for phytoplankton growth. If the role of

river discharge in the metabolism of western Lake Erie is to be understood, the pertinent facts will have to be compiled and analyzed over a period of several years. The following discussion presents these facts for 1942.

Six rivers contribute the major portion of the drainage water entering western Lake Erie, namely: St. Clair-Detroit, Huron, Raisin, Maumee, Portage, and Sandusky rivers. The location of these rivers and the size of their drainage areas have been described (Chandler 1944). Data concerning the volume of flow of the Huron River for 1942 were not available for the present report; thus when comparisons are made between discharge data for 1942 and previous years they are based on computations excluding the Huron River.

TABLE 2. River discharge into western Lake Erie, 1942, and percent contributed by individual rivers inclusive and exclusive of the St. Clair-Detroit River.

	Annual mean ft. ³ /sec.	Percent of total	Annual mean ft. ³ /sec.	Percent of total
St. Clair-Detroit	173,000	96.2
Raisin	781	0.4	781	11.4
Maumee	4,929	2.7	4,929	72.1
Portage	276	0.2	276	4.0
Sandusky	849	0.5	849	12.4
Total	179,835	100.0	6,835	99.9

The volume of flow of the St. Clair-Detroit River is much larger and more uniform (Table 2), and the water contains less suspended material than the discharge from the other rivers under consideration. The explanation for these differences lies in the fact that the source of water for the St. Clair-Detroit River is the upper Great Lakes instead of direct drainage from land areas as is the case of the other rivers. In 1942 the St. Clair-Detroit furnished over 96 percent of the water contributed by the rivers listed in Table 2; it supplied 98 percent in 1941 and 97 percent in 1940. Furthermore, its volume of flow is equivalent to about 90 percent of the discharge from the Niagara River, the outlet of Lake Erie.

In 1942 the discharge from the St. Clair-Detroit River was about 7 percent greater than in 1941. Its volume of flow was lowest in February with a monthly mean of 99,000 ft.³ per sec. It increased to 155,000 in March, to 182,000 in April, and reached the maximum of 189,000 in July. Following this maximum the flow decreased gradually to 177,000 ft.³ per sec. in December. Greater discharge in 1942 resulted from higher lake levels in the upper Great Lakes. This increased flow from the St. Clair-Detroit River appears to have caused lower water temperatures in April 1942 than in April 1941 by introducing a large volume of cold water from the more northern lakes and by increasing the general water level of the lake.

The combined discharge of the Raisin, Maumee, Portage, and Sandusky rivers in 1942 was less than

4 percent of that from the St. Clair-Detroit. This small percentage, however, affected the turbidities of the lake, because of the large amount of suspended materials which it contained. In 1942 the discharge from these rivers was 204 percent greater than in 1941; consequently more suspended matter entered the lake and greater turbidities resulted. Inspection of Figure 2 D shows that the large discharge from these rivers during winter and spring was accompanied by high lake turbidities at Put-in-Bay. This close correspondence between the degree of spring turbidity and the amount of spring river discharge is the usual occurrence in this lake. Autumn turbidities are often independent of river discharge as is the case in 1942. During this period turbidities are usually the result of storms which resuspend the bottom sediments through vertical turbulence. The effects of greater discharge from these rivers on lake levels and temperatures in 1942 were probably masked by the effects of the large volume of water from the St. Clair-Detroit River. There is evidence that nutrients in the lake are affected by the discharge from these four rivers which drain cultivated areas (Fig. 2 B).

TABLE 3. Run-off and precipitation, in inches, for the Maumee drainage basin, 1942.

1942	J	F	M	A	M	J	J	A	S	O	N	D	Total
Run-off	0.23	2.00	2.87	2.10	0.29	0.49	0.11	0.50	0.22	0.09	0.84	1.16	10.60
Precipitation	1.75	2.70	3.02	2.40	2.51	3.47	3.47	3.81	2.40	2.21	3.25	2.06	33.05

The Maumee drainage area has been chosen to illustrate the relation between precipitation and run-off in the southwest drainage basin, since the Maumee supplied 72.1 percent of the combined discharge of the four rivers above (Table 2). Total run-off for 1942 was 32.1 percent of the total precipitation (Table 3); for 1941 it was 12.5 percent. Seasonal variations are more marked than annual variations. From February through April, 1942, the run-off was 74 to 87 percent of the precipitation while in July it was only 3.1 percent. In 1941 this percentage varied from 30 to 43 from January through April. Run-off is generally greater during winter and spring months, not necessarily because of greater precipitation, but because of soil conditions. The soil at this time permits a minimum amount of infiltration due to the temperature conditions and to reduced cover. The foregoing data illustrate the well-established fact that meteorological conditions are partly responsible for annual variations in run-off for a given area. These variations in the amount of run-off are of particular interest to the present study in that they aid in explaining variations in lake turbidities, variations in the concentration of dissolved nutrients, and consequently variations in phytoplankton production.

LAKE LEVEL FLUCTUATIONS

The surface of Lake Erie does not remain at a uniform level but varies with year and season. The causes and extent of the changes in the surface level of the Great Lakes, over a period of 60 years, have

been investigated by Freeman (1926) and Horton & Grunsky (1927). According to the latter report, variations in lake level may be classified as natural or artificial. The natural causes are: (1) variations in rainfall and run-off from tributary areas, (2) variations in rainfall on and evaporation from the lake surfaces, (3) wind action, (4) barometric pressure variation, (5) ice obstruction of outlets, (6) seiches, (7) tides, and (8) tilting of the land surface. The artificial causes are: (1) regulation of outflow, (2) channel improvement, (3) diversion of water from the lake or tributary streams, and (4) deforestation and cultivation of lands in the drainage basin. In general the annual and seasonal variations in lake level are due to variations in rainfall and variations in the amount of evaporation from the lake surface. The permanent or secular changes in lake level are due to channel improvements, diversions, and a series of years of low rainfall and high evaporation. It is believed that variations in lake levels due either to an actual change in the volume of water in the lake, or to localized effects of seiches bring about changes in lake metabolism.

TABLE 4. Highest and lowest monthly and annual means of lake level, 1929-1942, Lake Erie at Cleveland.

Year	Highest monthly mean elev. in ft.	Month	Lowest monthly mean elev. in ft.	Month	Annual mean in ft.
1929...	574.27	June	571.83	Jan.	573.20
1930...	573.96	April	571.65	Dec.	573.05
1931...	571.69	July	570.70	Dec.	571.20
1932...	571.86	June	570.38	Dec.	571.29
1933...	572.11	May	570.12	Dec.	571.10
1934...	570.40	June	569.47	Dec.	569.99
1935...	570.89	Aug.	569.50	Feb.	570.24
1936...	571.19	June	569.43	Feb.	570.49
1937...	572.61	July	570.54	Dec.	571.57
1938...	572.29	July	570.56	Jan.	571.65
1939...	572.39	June	570.96	Feb.	571.68
1940...	572.28	July	570.61	Feb.	571.52
1941...	571.69	Jan.	570.50	Nov.	571.20
1942...	572.55	June	570.41	Jan.	571.78

Measurements of lake levels at Put-in-Bay were made by a self-registering Friez gauge, which was installed by the Detroit Lake Survey Office. Records were first obtained in late April, 1941, but the first complete year's record is that of 1942. The Cleveland records are complete from 1860 to date and since lake levels at Cleveland and Put-in-Bay are essentially the same, the former records were used for the preparation of Table 4. In this table only those records from 1929 to 1942 are considered since little limnological data are available for Lake Erie previous to this time. Also, the lake level in 1929 was the highest since 1900 and there is reason to believe that a similar height will be reached in 1943. This period then shows the general changes that occur from the time of one high level to the next. Years of high level are followed by years of low level, but with no predictable regularity. In general the highs and lows

of Lake Erie, both annually and seasonally, are the effects of meteorological conditions which prevail not only in its own drainage basin, but also in the drainage basins of all the Great Lakes above it. Inspection of Table 4 shows that the highest levels, based on monthly means, usually occur during summer and the lowest levels in winter.

TABLE 5. Number of lake level changes of 0.5 ft. or more in amplitude, arranged into six arbitrary groups, that occurred each week at Put-in-Bay, 1942.

Amplitude in feet	WEEK BEGINNING 1942															
	January				February				March				April			
	1	8	15	22	29	5	12	19	26	5	12	19	26	2	9	16
0.50-0.75	2	8	10	3	7	4	1	2	1	4	7	6	2	4	2	6
0.76-1.00	5	1	2	1	1	5	8	3	2	4	1	2
1.10-1.25	2	...	2	2	1	2	2	2	...	1
1.26-1.50	1	3	1	3	1	1
1.51-2.00	2	1	1	...	1	1	1	3
2.10-6.00	3	...	1	2	2

Amplitude in feet	WEEK BEGINNING 1942															
	May				June				July				August			
	7	14	21	28	4	11	18	25	2	9	16	23	30	6	13	20
0.50-0.75	7	8	4	17	12	7	9	8	10	6	16	10	5	7	4	8
0.76-1.00	3	5	4	5	...	3	4	...	12	3	3	1	6	3	...	6
1.10-1.25	1	...	2	2	...	2	...	5	...	1	...
1.26-1.50	1	...	3	1	...	2	...
1.51-2.00	...	1	3	...	1	...
2.10-6.00	...	1

Amplitude in feet	WEEK BEGINNING 1942															
	September				October				November				December			
	3	10	17	24	1	8	15	22	29	5	12	19	26	3	10	17
0.50-0.75	9	12	8	13	10	12	10	5	9	8	5	14	8	8	6	7
0.76-1.00	3	5	2	4	5	3	6	6	5	3	3	2	4	2	3	3
1.10-1.25	1	...	1	3	...	1	...	2	3	4	1	...	2
1.26-1.50	3	2	1	1	...	3	1	1	...	1	...	3	...	1
1.51-2.00	1	1	2	1	1	3	...	1	...	3
2.10-6.00	1	2	1	...	4

Inspection of Figure 1 A shows that marked weekly fluctuations in lake level occurred throughout the year. Most of these irregular changes in level may be attributed to the effects of seiches, while the more general changes are related to changes in the volume of the water in the lake. In 1942 the annual low in January was followed by a general increase until early March when an abrupt drop occurred. The ice cover had disappeared by this time and strong southwest winds produced several seiches (Table 5) that apparently account for this sudden drop. From March 5 to April 9 the level increased 1.87 ft. and this level was maintained with little change for five weeks. A further increase occurred in late May and this level corresponds with a period of increased discharge, especially by the St. Clair-Detroit River. A

maximum weekly mean of 572.60 ft. above mean tide at New York was reached during the week of July 25. This maximum was followed by a gradual decrease at first and then by irregular decreases as the autumn storms produced more seiches (Table 5).

Irregular increases and decreases in lake level due to seiches occur daily throughout the year. The importance of these fluctuations on lake biology is yet to be determined, but certain effects have been observed. Each seiche has two phases, one when the water level is rising and the other when the water level is falling. The number of changes in level of 0.5 ft. or greater, irrespective of direction, are recorded for each week in Table 5. These fluctuations in water level have been divided into the same arbitrary groups used in a previous paper (Chandler 1944). During the year, 649 fluctuations of an amplitude of 0.5 ft. or greater occurred and 124 of these exceeded 1.0 ft. Inspection of Table 5 shows that over 40 percent of these fluctuations of 1.0 ft. or greater occurred from September to December. The high lake turbidities at this time (Fig. 2 D) appear to be the result of resuspension of bottom sediments through the vertical turbulence which accompanies these seiches. The number and the seasonal distribution of seiches vary annually with meteorological conditions, especially with wind and barometric pressure.

At Put-in-Bay the amplitude of seiches varied from a few inches to 5.9 ft. in 1942. Amplitude of a seiche

is the difference in height between the maximum and the minimum water level during a complete oscillation (Henry 1902). There were 17 seiches with an amplitude exceeding 2.0 ft. and most of these occurred in January, November, and December. The largest seiche of the year is shown graphically for the entire lake in Figure 3. Some of the more important physical effects accompanying the larger seiches are: acceleration of shore erosion, resuspension of bottom sediments, production of currents, and exposure of bottom dwelling organisms of beaches and shoals.

TURBIDITY AND TRANSPARENCY

Turbidity values of the surface water near Put-in-Bay, based on weekly means, are shown in Figure 2 D. Weekly means were derived from daily readings. Frequent vertical readings were made, but in most instances values did not vary more than 5 ppm. from surface to bottom. On two occasions in April when temperature gradients existed, turbidity values varied as much as 20 ppm. from surface to bottom. Inspection of Figure 2 D shows that turbidity values were high during spring and autumn; the former period coincides with heavy river discharge and the latter with frequent storms (Table 5) that resuspended the bottom sediments. In general turbidities were much higher in 1942 than in 1941, especially during times of the year when phytoplankton production is usually the greatest. The highest daily value was 160 ppm.; this occurred on January 2 dur-

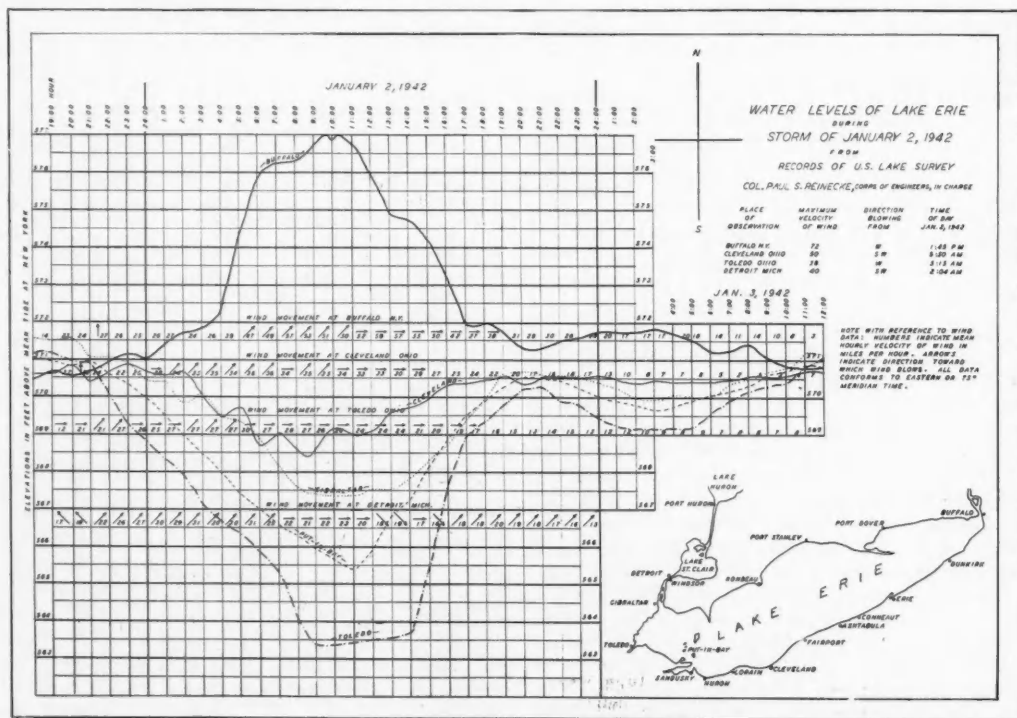


FIG. 3. Longitudinal seiche of Lake Erie.

ing the storm that produced the large seiche shown in Figure 3. Turbidities exceeded 100 ppm. only on three occasions and these occurred during heavy storms. The lowest daily value was 3 ppm. which existed for several days in June and July.

Turbidity values are not uniform throughout western Lake Erie; they are usually higher along the south shore where rivers and small streams enter the lake, and lower along the north shore because of the large volume of clear water discharged by the St. Clair-Detroit River. These clear and turbid waters along the shores are diverted at times by currents toward the central part of the lake. Horizontal studies of turbidity indicate that the values obtained at Put-in-Bay are representative of those existing in a large portion of western Lake Erie. In an attempt to supplement the daily readings at Put-in-Bay, use has been made of data collected by water filtration plants at Toledo and at Cleveland. The Collins Park Filtration Plant at Toledo receives its water from an intake crib in the lake about 3 miles off Little Cedar Point. At Cleveland the intake crib is about 5 miles off shore and is relatively free from the influence of river water. Data from these two filtration plants and from Put-in-Bay supply information on the conditions existing in the lake for a distance of about 100 miles.

At Toledo the weekly mean turbidity values from January to May varied from 7 ppm. to 478 ppm.; the average was 149 ppm. From May through December the weekly means varied from 10 ppm. to 135 ppm.; the average was much lower than during the former period. If a graph of the weekly mean turbidity values at Toledo were compared with a graph of the weekly mean discharge of the Maumee River a marked similarity in shape would be noted. In other words turbidities at the intake crib at Toledo are greatly affected by water from the Maumee River. Only occasionally were turbidity values higher at Put-in-Bay than at Toledo for corresponding periods. In general periods of high turbidities at Toledo were accompanied by increased turbidities at Put-in-Bay. This suggests that turbidities at Put-in-Bay are affected by the volume of discharge from the Maumee River.

The weekly mean turbidities at Cleveland were consistently lower than those at either Toledo or Put-in-Bay. From January to November the weekly mean values exceeded 20 ppm. only three times; these occurred in April with a maximum of 55 ppm. During November and December values varied from 12 to 42 ppm., the average being about 23 ppm. In general the weekly mean values at Cleveland closely resemble the graph of turbidity at Put-in-Bay (Fig. 2 D), except values at the latter place are consistently higher.

Turbidities are higher in western Lake Erie than in the remainder of the lake because the western end receives large quantities of tributary water, and its shallowness permits resuspension of bottom sediments through vertical turbulence. When this turbid water of western Lake Erie moves eastward it clears because of dilution and sedimentation.

Secchi disc readings varied from 0.2 m. in April when the turbidity was 130 ppm. to 3.4 m. in June when the turbidity was 4 ppm. Data collected in 1942 and in previous years (Chandler 1944) suggest that the disc is not a satisfactory instrument for measuring transparency in this lake because of the varying types of suspended materials in the water.

Depths to which 1.0 percent of the surface light penetrated during the year varied from 1.7 m. when the turbidity was 130 ppm. to 8.5 m. when the turbidity was 4 ppm. In general, 1.0 percent of the surface light penetrated to depths of 5 m. or less when turbidities exceeded 15 ppm. and to depths of 3 m. or less when 25 ppm. or greater. If the depth to which 1.0 percent of the surface light penetrates is accepted as the lower limit of the euphotic zone then this zone was restricted to the upper 2 or 3 m. from early March to early May, the period when phytoplankton production is usually the greatest.

CHEMICAL CONDITIONS

Chemical analyses of the lake water in the Bass Islands region during 1942 included measurements of dissolved oxygen, ammonia-nitrogen, nitrite-nitrogen, and nitrate-nitrogen. During the last half of the year phosphate-phosphorus determinations were made on the lake water both before and after complete oxidation of the organic matter. With the exception of dissolved oxygen determinations all of the analyses were made on composite samples prepared from the surface and from 5 and 9 m. depths. All of the samples were taken from one location in the 1,000-acre area customarily investigated (Chandler 1940). This is the same area from which samples were taken for phytoplankton enumeration.

The method used for measuring dissolved oxygen was the same as in previous years. The inorganic-nitrogen constituents were determined according to the procedures given in American Public Health Association (1936). Nitrate-N was measured by the phenol-disulfonic acid method rather than by reduction techniques. Oxidation of organic matter and subsequent measurement of phosphate-P were done according to the method of Robinson & Kemmerer (1930). The concentration of phosphate-P after oxidation represents the total phosphorus (Juday, Birge, Kemmerer, & Robinson 1927). Phosphate-P not in organic combination, the so-called "soluble-phosphorus," was determined by the Atkins' modification (1923) of Deniges' ceruleomolybdate method. Since the lake water was filtered through only a coarse filter paper (Whatman No. 1) prior to soluble phosphate-P determinations, the amounts which are given may include some of the acid-soluble sestonic phosphate-P fraction (Hutchinson 1941). "Organic"-P is the difference between total-P and soluble phosphate-P and therefore may include phosphorus not in pentavalent form before oxidation of the organic matter. All of the chemical analyses were completed within 6 hours of the time of collection.

OXYGEN

Concentrations of dissolved oxygen in the surface layer of water as well as at 5 and 9 m. were similar to those reported for other years (Chandler 1940, 1942a, 1944). Slight differences were found frequently in the oxygen content of the three layers, but these usually did not exceed 2 mg. per liter. Oxygen values for the entire column of water, expressed in terms of percent saturation for an elevation of 210 m., ranged from 82.1 percent to 103.5 percent during 1942. Conditions of supersaturation were observed on several occasions. On July 15 the supersaturation was restricted to the water above the 5 m. layer, and it occurred simultaneously with temporary thermal stratification of the water. The most pronounced supersaturation was observed on September 1 when the surface layer of lake water was 120.2 percent saturated, and the supersaturation extended to the 5 m. layer where values of 100.5 percent saturation were found. On this date the autumn phytoplankton pulse reached its peak and the lake was exceptionally calm. Saturation occurred during November; during this period the oxygen was distributed in a uniform manner vertically as the result of turbulence. The lowest values were found during July and August, and this corresponds with the findings of previous years. Since oxygen determinations were seldom made on more than two dates in one month, and since the 1942 data are generally similar to more complete data which have been published, the data for 1942 are not tabulated in this report.

PHOSPHORUS

Frequent determinations of total and soluble phosphate-P were started the last of July, 1942. The amounts of "soluble" and "organic"-P are plotted in terms of the element in Figure 2 A. The original data are recorded in Table 6. Inspection of these data shows that "organic"-P varied from a high of 26 μg per l on August 26, coincident with the period of highest phytoplankton population, to a low of 2 μg per l on September 18 coincident with a sudden decrease in the amount of phytoplankton. The three maxima which are to be seen in the "organic"-P curve occurred at the same time as the peaks in the autumn phytoplankton population. Decreases in the phytoplankton numbers likewise were accompanied by decreases in "organic"-P. A more exact interpretation is difficult since sampling dates for phosphorus determinations and for phytoplankton enumerations did not coincide always. The direct relationship indicated by these data was not found by Juday, Birge, Kemmerer, & Robinson (1927) nor by Tressler & Domo-galla (1931) in their studies of Wisconsin lakes.

Soluble phosphate-P values varying from 1 to 8 μg per l were found for the period studied in 1942. The high value was found on three occasions: (1) August 26, at the time of the greatest "organic"-P concentration; (2) September 25, during a period of increased turbidity which was apparently due to increased river discharge; and (3) on and after December 10, two weeks following cessation of the autumn

TABLE 6. Inorganic nitrogen and phosphorus of western Lake Erie, 1942.

Date 1942	Micrograms per liter							Relative concentration (percent total N or P)			
	NH ₃ -N	NO ₂ -N	NO ₃ -N	Total inorganic-N	Soluble phosphate-P	"organic"-P	Total-P	NH ₃ -N	NO ₂ -N	NO ₃ -N	PO ₄ -P
Apr. 27	130	130
May 11	120	1400	1520	7.9	92.1
25	44	2	1300	1346	3.3	0.2	96.5
June 9	32	4	300	336	9.5	1.2	89.3
18	68	2	250	320	21.1	0.6	78.3
29	96	14	400	510	18.8	2.7	78.5
July 3	64	20	400	484	13.2	4.2	82.6
10	40	14	250	304	13.1	4.6	82.3
17	24	10	100	134	17.9	7.5	74.6
23	40	10	100	150	26.6	6.7	66.6
31	56	7	70	133	4	6	10	42.1	5.3	52.6	40.0
Aug. 7	40	8	70	118	2	14	16	33.9	6.7	59.4	12.5
13	16	5	50	71	6	10	16	22.5	7.0	70.5	37.5
21	16	3	35	54	2	18	20	29.6	5.5	65.0	10.0
26	24	7	30	61	8	28	36	39.4	11.5	49.3	22.0
Sept. 3	8	0	30	38	6	14	20	21.0	0.0	79.0	30.0
11	12	0	0	12	2	8	10	100.0	0.0	0.0	20.0
18	16	3	30	49	1	2	3	32.6	6.1	61.3	33.0
25	28	5	30	63	8	9	17	44.5	7.9	47.6	47.0
Oct. 2	16	2	30	48	4	4	8	33.4	4.1	62.5	50.0
9	16	0	70	86	1	5	6	18.6	0.0	81.4	16.7
15	20	0	0	20	1	13	14	100.0	0.0	0.0	7.0
28	16	2	70	88	4	12	16	18.2	2.2	79.6	25.0
Nov. 4	16	2	75	93	2	14	16	17.2	2.2	80.6	12.5
16	20	10	80	110	2	14	16	18.2	9.2	72.6	12.5
25	20	300	320	4	6	10	6.3	93.7	40.0
30	40	38	400	478	6	6	12	8.4	8.0	83.6	50.0
Dec. 10	40	10	300	350	8	6	14	11.4	2.9	85.7	57.0

phytoplankton pulse. The lowest values for soluble phosphate-P were found during the first half of September and during the second and third weeks of October. The low values of September occurred as the phytoplankton population was decreasing, while those of October came when phytoplankton numbers were increasing. An inverse relationship between "organic"-P and soluble phosphate-P is generally apparent for most of this autumn period, and the exceptions which do occur are not easily explained. On September 25, the rapid increase in both phosphorus fractions was due partially to an influx of turbid water from the southwest drainage area. However, the increase in soluble phosphate-P at this time might have been due in part to an increase in ferric phosphate (acid-soluble sestonic phosphate, Hutchinson 1941), and it would not, therefore, represent an actual increase in soluble phosphate-P.

The mean soluble phosphate-P content of the lake water during the last half of 1942 was 3.9 μg per l, and this is similar to the mean of 0.003 mg. per l (3.0 μg) reported for 479 northeastern Wisconsin lakes by Juday & Birge (1931). However, the mean soluble phosphate-P concentration of the surface water in Linsley Pond was found by Hutchinson (1941) to be only 0.0017 mg. per l. Between 7 and 57 percent of the total phosphorus found for western Lake Erie in 1942 was in the soluble phosphate-P

form; the mean was 29 percent. A considerably greater proportion of the total phosphorus was in the soluble fraction in western Lake Erie than in Linsley Pond, where Hutchinson found about 8 percent in the soluble form, or in certain lakes of Wisconsin where Juday and Birge found approximately 12 percent of the phosphorus in the soluble fraction. Data for the Gulf of Maine (Redfield, Smith, & Ketchum 1937) show that between 70 and 90 percent of the total phosphorus found was in the soluble form.

The cycle of phosphorus in relatively stable water masses has been considered by Hutchinson (1941) for Linsley Pond and by Redfield, Smith, & Ketchum (1937) for the Gulf of Maine. The shallow, non-stratified western Lake Erie presents a different picture than that considered by these and other investigators. It has been found (unpublished data) that the horizontal distribution of most of the inorganic compounds, including those of phosphorus, in western Lake Erie varies more than the vertical distribution. There is a certain intermingling of the different areas due to wind and to eddy currents around the islands as the water moves eastward at a rate of approximately 0.1 m.p.h. Once in each 24-hour period the entire volume of water in the one area most extensively studied could be completely replaced. This situation makes it practically impossible to apply the reasoning of Harvey (1934) to estimate total phytoplankton production from phosphorus consumption, or to state that biological utilization is the cause of the decreases in the concentration of non-conservative elements. Again, the shallowness of the lake prevents the accumulation of deep water reserves of phosphorus, and the presence of an oxidized zone at the mud-water interface should present an almost impassable barrier to regeneration of phosphorus through pelometabolism (Einsele 1936; Hutchinson 1941). Phosphorus brought into the lake in particulate form or that fixed in the plankton would be lost as the result of sedimentation. This apparently unfavorable balance in the phosphorus cycle seems to be offset by a constant supply of phosphate-P from the southwest drainage area and from the upper Great Lakes, plus that which is regenerated by limnetic processes. The importance of these last processes in western Lake Erie is not known, but investigations in other places have shown phosphorus liberation to be a relatively rapid reaction (Cooper 1935). It would seem therefore that the cycle of phosphorus in western Lake Erie is not as closed as the one in Linsley Pond, and that paralimnetic factors play a more important role in western Lake Erie.

INORGANIC NITROGEN

Weekly determinations of the inorganic nitrogen content of a composite sample of lake water were begun, under the present program, in May, 1942. Total inorganic-N data are plotted in Figure 2 along with phytoplankton numbers and lake water turbidities. The inorganic-N constituents from which the total values were derived are included in Table 6. A

brief discussion of the seasonal distribution of the inorganic-N constituents will serve to describe the seasonal distribution of total inorganic-N.

Nitrate-N was the most plentiful form of inorganic-N measured, and nitrite-N was the least. During the part of 1942 studied the amount of nitrate-N varied from 0 to 1,400 μg per l, ammonia-N from 8 to 120 μg per l, and nitrite-N from 0 to 38 μg per l. Relatively large amounts of nitrate-N were found during May, June, and the first two weeks of July. During this time the amounts always exceeded 100 μg per l and usually 200 μg per l. Following the second week of July and until the third week of November, the amount of nitrate-N was always less than 100 μg per l and usually less than 70 μg per l. After November 15 nitrate-N values increased abruptly to between 300 and 400 μg per l, and this level was maintained throughout December. In general, periods during which the largest amounts of nitrate-N were found were also the periods during which the largest amounts of ammonia-N and nitrite-N were found. In the period from May through July, ammonia-N values varied from 24 to 120 μg per l and nitrite-N values from 2 to 20 μg per l. From August through October, ammonia-N amounts varied from 8 to 40 μg per l and nitrite-N values from 0 to 8 μg per l. After the first week of November ammonia-N and nitrite-N concentrations increased rapidly. The former increased from 16 to 40 μg per l while the latter increased from 2 to 38 μg per l.

When the relative concentrations of the inorganic-N components were compared with the absolute concentrations the following situation was found. The largest relative concentrations of ammonia-N and nitrite-N (Table 6) occurred during July, August, and September rather than when the largest absolute concentrations were found in the spring and late autumn months. Presumably this relationship is due to the decrease in amounts of inorganic-N introduced from the southwest drainage area since most of this is in the form of nitrate-N when it reaches the area of the Bass Islands.

When a comparison is made between the curve of total inorganic-N and the curve of total phytoplankton numbers (Fig. 2 B, C) a relationship appears to exist. The relatively small concentrations of inorganic-N from late July to October may be attributed in part to plankton utilization, and the increased amounts of inorganic-N observed in the late spring and in the winter could be assigned to biological regeneration. It is difficult, however, to know how much importance must be given to biological processes and how much to meteorological factors when an explanation of the fluctuations in biologically effected elements is attempted. Additional data which are available for western Lake Erie seem to indicate that meteorological factors play a considerable role in accounting for the variations observed in the concentrations of inorganic-N and phosphorus.

During 1939 and 1940 extensive chemical analyses were made (by L. Bodenlos of the Stone Laboratory

staff) at weekly intervals on water samples taken from the same area of western Lake Erie as that considered in this paper. These unpublished data include ammonia-N, nitrite-N, and nitrate-N content of samples taken from three depths. While detailed consideration of these data is reserved for future publication, certain aspects of the findings will be dealt with here. The incomplete data for 1942 compare well with the findings for the seasonal distribution of inorganic-N in the earlier two years. The high nitrate-N value of May, 1942, were approximately equaled during May, 1939, and 1940. In addition the months from February to May of the earlier years were characterized by high concentrations of inorganic-N, especially nitrate-N. In both 1939 and 1940, as in 1942, the lowest concentrations of the year were found during the period from August to October, but here the similarity ceases. In an attempt to explain the annual variations in amounts of inorganic-N, a comparison is made between the seasonal distribution of inorganic-N and river discharge.

The monthly means of the total inorganic-N obtained from the values for 1939, 1940, and 1942 are plotted in Figure 4 along with the combined monthly mean discharge of the Maumee and Portage rivers for the same years, and also with the monthly mean discharge of the St. Clair-Detroit River for this period. The Maumee and Portage rivers were chosen to represent the southwest drainage system. Data for the St. Clair-Detroit River are also included since this discharge, derived directly from the upper Great Lakes, makes up by far the greatest volume of water coming into Lake Erie. There is a marked similarity between the shape of the curve illustrating seasonal distribution of inorganic-N and that illustrating sea-

sonal distribution of the Maumee and Portage rivers' discharge. The greatest discharge of the Maumee and Portage rivers, during the period considered, occurred in the spring months when they frequently reached flood stage. Immediately following this period the highest values for total inorganic-N were found. This was also the period of greatest increase in the discharge of the St. Clair-Detroit River, and such an increase may have played a part in the increases found for inorganic-N. While the discharge of the Maumee and Portage rivers was decreasing during the summer months toward the minimum value of September and October, the amounts of inorganic-N were decreasing toward their minimum monthly values. The discharge of the St. Clair-Detroit River does not show this same trend. The discharge of the Maumee and Portage rivers increased after October and so did the amounts of inorganic-N. All of the data which are available indicate that drainage from surrounding land areas is an important source of plant nutrients for western Lake Erie. This reservoir is important to the lake biology since, as was previously stated, the shallowness of western Lake Erie does not permit the accumulation of deep water reserves.

The seasonal distribution of inorganic-N in western Lake Erie is similar to that found for other bodies of fresh water. The highest values are found during the spring and winter months, and the lowest values during the late summer months. In certain Wisconsin lakes the increase in amounts of nitrate-N during spring months was thought to be due entirely to bacterial activity (Domogalla, Fred, & Peterson 1926). The influence of spring water rich in nitrate-N was considered, but with the possible exception of Lake

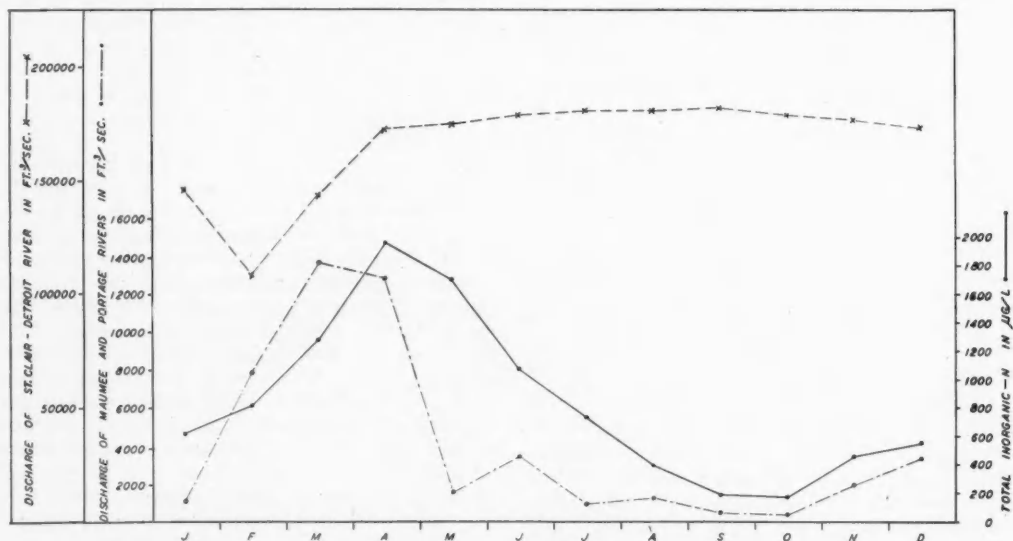


FIG. 4. Monthly mean inorganic-N of the lake water, combined monthly mean discharge of the Maumee and Portage rivers, and the monthly mean discharge of the St. Clair-Detroit River. Monthly means are based on data of 1939, 1940, and 1942.

Wingra only a small portion of the increases observed in March and April could be accounted for by the inflowing waters. Tressler & Domogalla (1931) concluded from a detailed study of Lake Wingra that increases in ammonia-N and nitrate-N during spring months were due to the increased bacterial activity resulting from a rise in temperature. During a study of some English lakes Pearsall (1930) also found increased amounts of plant nutrients during the period from November to June. Factors such as land drainage, complete circulation of the lake water, and decreased rates of denitrification due to lower temperatures were listed by him to explain the increases which occurred. Pearsall (1923) previously had stressed the importance of land drainage in producing increases in the concentration of inorganic compounds in lake water, especially in lakes having a predominantly soil-covered drainage area.

PHYTOPLANKTON

Each collection of water from which the standing crop of phytoplankton was determined consisted of a composite sample containing 1 liter from each of the following: the surface, the 5 m. depth, and the 9 m. depth. Collections were made at intervals of 7 to 12 days throughout the year in the same area studied in previous years (Chandler 1940, 1942a, 1944). An arbitrary method designed to partially correct for differences in volume of the various plankters was used in the enumeration of phytoplankton. Abundance is expressed in units per 1. The following have been considered as one unit: 1 cell of *Mallomonas*, *Amphiprora*, *Cyclotella*, *Cymatopleura*, *Cymbella*, *Gomphonema*, *Gyrosigma*, *Stephanodiscus*, *Surirella*, *Synedra*, *Closteriopsis*, *Closterium*, *Cosmarium*, and *Staurastrum*; 1 colony of *Aphanocapsa*, *Aphanothece*, *Chroococcus*, *Coelosphaerium*, *Gomphosphaeria*, *Microcystis*, *Botryococcus*, *Coelastrum*, *Dietiosphaerium*, *Oocystis*, *Pediastrum*, and *Wetzelia*; 4 cells of *Rhizosolenia*, *Quadrigula*, *Scenedesmus*, *Schroederia*, and *Selenastrum*; 5 cells of *Dinobryon*; 6 cells of *Ankistrodesmus*; 8 cells of *Asterionella*, and *Tabellaria*; 16 cells of *Merismopedia*; 100 μ of *Fragilaria*; 300 μ of *Anabaena*, *Aphanizomenon*, *Oscillatoria*, *Tribonema*, *Diatoma*, and *Melosira*. Pulse level for populations of the total phytoplankton has been placed at 50,000 units per 1 for reasons stated in a previous paper (Chandler 1942a). Comparisons between phytoplankton abundance in different years and between seasons of the same year are based on planimetric integration of graphs showing the standing crop at intervals of 7 to 12 days. The areal figure thus obtained is used in this paper to represent the size of the phytoplankton population for a unit of time, and when applied to a year it is called the annual crop, and when applied to seasons it is referred to as the spring crop or the autumn crop. Percentage composition of individual collections (Table 7) was determined directly from the number of phytoplankton units per 1.

Well defined spring and autumn pulses occurred

during the year (Fig. 2 C). The spring pulse began February 10 and terminated on April 12, a duration of 9 weeks, and it constituted 28.6 percent of the annual crop. It may be noted that its inception occurred during the presence of an ice cover and it coincided with the seasonal increase in solar radiation (Fig. 1C). The early stages of the pulse indicated that it would attain large proportions before its completion, but a sudden termination ensued coincident with the disappearance of the ice cover, and with high turbidities due to wind action and river discharge (Fig. 2 D). Composition of the pulse was 94 percent diatoms, 4 percent greens, and 2 percent blue-greens. A comparison of this pulse with the 1941 pulse, the largest thus far observed, shows the following facts: (1) duration of the 1942 pulse was 40 percent shorter than in 1941; (2) maximum number of units per 1 was about 53 percent less in 1942; (3) size of the 1942 pulse was about 19 percent of that in 1941; and (4) *Asterionella* was the predominant form during both springs.

TABLE 7. Percent composition of phytoplankton for individual collections.

1942	Blue-greens	Diatoms	Greens	1942	Blue-greens	Diatoms	Greens
Jan. 14..	6.6	90.4	2.9	July 22..	45.6	30.2	24.2
24..	2.4	92.1	5.4	Aug. 5..	51.1	27.8	21.1
Feb. 10..	3.2	92.1	4.7	13..	39.0	44.9	16.1
20..	1.3	88.1	10.6	21..	45.7	31.2	23.1
25..	2.1	94.0	3.9	27..	16.0	78.0	6.0
Mar. 5..	2.1	87.8	10.0	31..	13.2	81.9	4.8
10..	0.8	95.7	3.4	Sept. 5..	18.6	78.7	2.7
19..	0.3	98.1	1.5	21..	14.0	79.8	6.2
27..	3.0	95.3	1.6	29..	15.8	81.4	2.8
Apr. 9..	10.2	85.2	4.6	Oct. 9..	19.7	75.6	4.7
15..	6.8	80.9	3.3	15..	8.6	86.6	4.8
22..	9.6	83.3	7.0	28..	12.8	86.2	1.0
May 11..	6.1	90.2	3.7	Nov. 5..	29.7	68.6	1.6
26..	5.5	93.9	0.5	16..	9.6	90.3	0.0
June 3..	8.1	89.4	2.5	30..	6.7	79.1	14.1
18..	3.1	92.6	4.3	Dec. 10..	3.0	97.0	0.0
July 15..	39.1	32.7	28.2				

The second pulse of the year began July 15 and terminated November 20, a duration of 19 weeks (Fig. 2 C). It constituted about 54 percent of the annual phytoplankton crop. Composition of the entire autumn population was 76 percent diatoms, 4 percent greens, and 20 percent blue-greens. Composition of individual collections is shown in Table 7. A comparison of the 1942 autumn pulse with that of 1941 shows the following: (1) duration of the 1942 pulse was 10 percent longer than in 1941; (2) maximum number of units per 1 was 15 percent greater in 1942; (3) the size of the 1942 pulse was 14 percent smaller than in 1941; and (4) diatoms composed 76 percent of the 1942 pulse in contrast to 43 percent in 1941.

Phytoplankton populations existing between the above described pulses constituted about 17 percent of the annual crop and diatoms were the dominant forms except in July and August. This fact explains the emphasis which has been placed on pulse periods.

The spring phytoplankton pulse off Cleveland (based on data obtained from the Division Filtration Plant) began March 10, reached its maximum early in April, and then decreased to a low level in late April and early May. A secondary pulse occurred from mid-May to mid-June. The number of weeks during which pulse proportions existed was 12. This is about the same as in 1941. The 1941 pulse, however, was more than three times greater in size than the one in 1942, but both were dominated by diatoms. The autumn pulse began August 28 and terminated December 19, a duration of 16 weeks. It was composed essentially of diatoms, but greens and blue-greens were much more abundant than during spring.

Studies of the phytoplankton populations at Put-in-Bay and at Cleveland during 1942 confirm earlier observations in respect to the following facts: (1) in general both spring and autumn pulses begin earlier at Put-in-Bay than at Cleveland, but the over-all duration is about the same; (2) composition of the spring phytoplankton is similar at the two stations; (3) greens and blue-greens compose a greater percentage of the autumn phytoplankton at Put-in-Bay than at Cleveland; and (4) annual variations in the abundance of phytoplankton are greater at Put-in-Bay than at Cleveland and this is due in part to higher and more irregular turbidities at Put-in-Bay.

MYXOPHYCEAE

This group composed about 2 percent of the spring phytoplankton and about 20 percent of that in the autumn. Blue-greens were present in all collections of the year, but from January to mid-July they did not exceed 8,000 units per 1, nor did they compose more than 10.2 percent of any one collection (Table 7). During the second half of the year this group was much more abundant, and it reached a maximum of 68,000 units per 1 in late August. Blue-greens were not nearly as abundant in 1942 as in 1941. In 1942 the following genera listed in order of their abundance made up most of the autumn blue-green population: *Aphanizomenon*, *Merismopedia*, *Coelosphaerium*, *Chroococcus*, and *Microcystis*. The following is a description of the seasonal abundance of the more common genera of blue-greens.

Anabeana appeared in most collections from July to early September, but at no time did it exceed 2,000 units per 1. In other years this plankton has formed heavy blooms in the protected bays, but in 1942 a bloom did not appear.

Aphanizomenon and *Oscillatoria* were combined in making quantitative counts. They occurred in most collections during the year but from January to July their greatest abundance was 3,000 units per 1. A definite pulse appeared in mid-July and reached a maximum of 36,000 units per 1 in mid-August. During the pulse these forms were exceeded in abundance only by *Melosira*.

Aphanocapsa appeared in collections during August and early September; the greatest number of units per 1 was 1,200.

Aphanothece occurred irregularly in collections

during July and August; its maximum was 1,000 units per 1.

Chroococcus was present in most collections, but the greatest abundance occurred from late July to mid-September; a maximum of 8,000 units per 1 appeared in late August. This genus ranked fourth in abundance among the blue-greens.

Coelosphaerium was present from late July to early November; a maximum of 17,700 units per 1 occurred in late August. This form ranked third in abundance among the blue-greens.

Gloeotrichia did not exceed 1,000 units per 1 at any time and its presence was limited to three weeks in August.

Gomphosphaeria occurred in three collections in August; its maximum was 1,200 units per 1.

Merismopedia appeared in collections only from late July to mid-October. A maximum of 21,500 units per 1 occurred in late August. This form ranked second in abundance among the blue-greens.

Microcystis was present in collections from mid-July to early October; a maximum of 4,700 units per 1 occurred in late August. This genus ranked fifth in abundance among the blue-greens.

CHRYSPHYCEAE

Dinobryon occurred during April, but it did not exceed 1,100 units per 1.

Mallomonas was present in three collections in June, but in quantities less than 1,200 units per 1.

HETEROPHYCEAE

Botryococcus was found irregularly in collections from July to September; its greatest abundance was 1,700 units per 1 in August.

Tribonema occurred during August in quantities less than 1,200 units per 1.

BACILLARIOPHYCEAE

Diatoms composed a large percentage of each phytoplankton collection during the year (Table 7) except during July and August; therefore, the graph of total phytoplankton shown in Figure 2 C characterizes the seasonal abundance of diatoms. Diatoms during the spring pulse composed 32 percent of the annual diatom crop. *Asterionella* constituted 86 percent of this diatom pulse and the remaining 14 percent was composed primarily of the following genera listed in order of their abundance: *Synedra*, *Tabelaria*, *Fragilaria*, *Melosira*, and *Stephanodiscus*.

The autumn pulse of diatoms in 1942 was the largest recorded during a period of four years, and it composed about 52 percent of the annual crop of diatoms. *Melosira* constituted about 85 percent of this autumn pulse and the remaining 15 percent was made up essentially of the following genera listed in order of their abundance: *Fragilaria*, *Stephanodiscus*, *Asterionella*, *Synedra*, and *Tabellaria*.

Diatoms were as predominant in the plankton at Cleveland as they were at Put-in-Bay. The data for Cleveland are not adequate for accurate determination of the percentages that each plankton group composed of the total. Rough calculations show that

diatoms composed 98 percent of the spring phytoplankton and about 94 percent during the autumn. During the spring pulse *Asterionella* and *Melosira* were nearly equal in abundance and together they constituted about 77 percent of the total diatom population. The remaining 23 percent was composed of the following genera listed in order of their abundance: *Synedra*, *Stephanodiscus*, *Tabellaria*, and *Fragilaria*. About 75 percent of the autumn diatom pulse was made up of *Melosira* and the remaining 25 percent was composed of the following genera listed in order of their abundance: *Synedra*, *Asterionella*, *Stephanodiscus*, and *Tabellaria*. The following is a description of the seasonal abundance of the more common genera of diatoms at Put-in-Bay.

Amphiprora was found only during April; its maximum abundance was 1,770 units per 1.

Asterionella was present in most collections during the year, but only one pulse occurred and that was from early February to late May. This plankter made up about 86 percent of the spring diatom population and it reached a maximum of 410,000 units per 1 in mid-March. Following the spring pulse it occurred in irregular quantities, not exceeding 13,000 units per 1, for the remainder of the year. *Asterionella* is generally the predominant plankter each spring in western Lake Erie and this may be explained in part by the competitive advantage it attains by maintaining a larger winter population than other phytoplankters.

Cyclotella and *Stephanodiscus* have been combined in making quantitative counts because of the difficulty in distinguishing one from the other at times of high lake turbidities. During 1942 *Stephanodiscus* was more numerous than *Cyclotella*. From January to mid-March these forms were seldom encountered in the plankton, but a small pulse occurred from late March to late April with a maximum of 9,600 units per 1. A second pulse occurred from mid-August to mid-September with a maximum of 14,000 units per 1. Between the two pulses these forms when present did not exceed 1,200 units per 1.

Cymatopleura occurred in a few collections during August and September; the maximum was 1,200 units per 1.

Cymbella was found in several collections during March and April; the maximum was 1,700 units per 1.

Diatoma was present during March and April and its maximum abundance was 4,700 units per 1.

Fragilaria occurred in all collections of the year, but two peaks of abundance existed, the first during March and April with a maximum of 5,000 units per 1, and the second from July to December with a maximum of 86,000 units per 1 in November.

Gomphonema appeared in collections during September and October; the maximum abundance was 1,200 units per 1.

Gyrosigma occurred in several collections during August and September, but it did not exceed 1,200 units per 1.

Melosira was in all collections during the year, but

from January to mid-August it did not exceed 6,000 units per 1, except for two collections in May. From mid-August to mid-November a definite pulse occurred; the maximum was 394,000 units per 1 in early September. *Melosira*, an important constituent of the autumn plankton each year, was about twice as abundant in 1942 as in any previous year.

Rhizosolenia was present in collections from February to mid-April, but the maximum recorded was 2,300 units per 1. High lake turbidities during most of this period interfered with accurate determination of its abundance.

Stephanodiscus. See description of *Cyclotella*.

Surirella was found in only one collection in April; the quantity was 600 units per 1.

Synedra was most abundant from January to June; the maximum during this period was 17,000 units per 1. From June to December this form was encountered only occasionally and it did not exceed 2,000 units per 1. *Synedra* was less abundant during 1942 than in any of the four previous years.

Tabellaria occurred in all collections except those of August, September, and October. A small spring pulse occurred from February to May; the maximum was 10,000 units per 1 in March.

CHLOROPHYCEAE

Green algae occurred in most collections throughout the year, but from January to July the maximum number per 1 was 8,000 units. During this period they composed no more than 11 percent of any one collection and the average percentage was 4 (Table 7). From July to late September a pulse occurred with a maximum of 31,800 units per 1 in late August. In general, members of this group were more numerous during the spring of 1942 than in previous springs, but their abundance during the autumn of 1942 was about the same as in previous years. The six genera of greens that constituted the major portion of the autumn pulse listed in order of their abundance are as follows: *Dictyosphaerium*, *Schroederia*, *Scenedesmus*, *Pediastrum*, *Oocystis*, and *Coelastrum*. The following is a brief description of the seasonal abundance of the more common genera that occurred in the plankton.

Ankistrodesmus made up about 95 percent of the green algae present from January to June. The maximum abundance during this period was 8,000 units per 1. From June to December it was absent in all collections except one.

Closteriopsis was present in several collections from mid-May to August, but at no time did it exceed 1,200 units per 1.

Coelastrum was present from mid-July to October and a maximum of 1,500 units per 1 occurred in late July.

Dictyosphaerium occurred in collections from July to mid-October with a maximum of 13,000 units per 1 in late August.

Oocystis was present from mid-August to mid-September and the maximum abundance was 8,200 units per 1 in late August.

Pediastrum made its first appearance in June collections and was found in subsequent collections until October. The maximum abundance was 5,500 units per 1 in July.

Quadrigula occurred in July and August collections; the maximum quantity was 3,000 units per 1.

Scenedesmus was found in most collections throughout the year; the period of greatest abundance was from July to October with a maximum quantity of 4,700 units per 1. Preceding and subsequent to this period *Scenedesmus* occurred in irregular quantities varying from 600 to 2,000 units per 1.

Schroederia occurred in all collections from June to December, but the maximum of 5,900 units per 1 occurred in late August.

Selenastrum was found in July and August collections; its maximum quantity was 1,200 units per 1.

Staurostrum occurred during July and August collections, but at no time did it exceed 1,800 units per 1.

Westella was present in the July and August collections and its maximum was 2,000 units per 1.

DISCUSSION

The production of phytoplankton in western Lake Erie during 1942 differed from that of previous years in many respects as did the limnological and meteorological factors which directly or indirectly affected this plankton. Since results for each year from these year-round studies have been different the need for their continuation is apparent. Until a greater knowledge of the extent of the annual variations is acquired any attempt to generalize on the basis of observations limited to one season or even a complete year will have little meaning. A comparison of the phytoplankton populations of four consecutive years in respect to the size of seasonal and annual crops lends support to the above statement. If the phytoplankton crop of 1941 is assigned the value of 100 then the annual crops expressed in percent of the 1941 crop are: 1939, 47 percent; 1940, 29 percent; and 1942, 45 percent. The spring crops are: 1939, 17 percent; 1940, 25 percent; and 1942, 19 percent. The autumn crops are: 1939, 98 percent; 1940, 23 percent; and 1942, 86 percent. Had studies been limited to any one of these years our impression of phytoplankton production in this lake would have been greatly distorted; this distortion would have been even greater if studies were limited to a single season. It is possible that annual variations in the production of phytoplankton in western Lake Erie are greater than those which occur in smaller inland lakes; however, this cannot be stated with certainty because of the lack of comparable data.

Phytoplankton is not the only group of organisms in this lake that exhibits wide annual fluctuations in abundance. It is a well-established fact that the abundance of commercial species of fishes varies greatly from year to year (International Board of Inquiry 1943). Unpublished data at this laboratory show considerable annual variations in the abundance of microcrustaceans, rotifers, nymphs of mayflies of the genus *Hexagenia*, and larvae of certain midges.

At present it is not possible to state the relationship between the annual variations in the abundance of one group with that of another, but there is evidence that these variations are caused by factors common to all groups. Doan (1942) has shown that the abundance of certain fishes in western Lake Erie is related to prevailing meteorological and limnological conditions. The same conditions have been shown to control annual abundance of phytoplankton (Chandler 1942a, 1944).

The principal factors controlling phytoplankton production in the ocean (Sverdrup, Johnson, & Fleming 1942) are: (a) direct primary factors that operate directly on the growth and reproduction of the individual alga; and, (b) direct secondary factors that directly influence the population density and, therefore, the total production which is possible in a given time. The direct primary factors are: solar energy, supply of nutrients, accessory growth substances and factors influencing metabolism. The direct secondary factors are: consumption by herbivorous plankters, sinking, and vertical transport. In addition to these direct factors there are several indirect secondary ones which operate simultaneously with the direct primary and the direct secondary factors. Among these indirect factors may be listed: water movements of various kinds, stability of water in the euphotic zone, river discharge, meteorological conditions, bathymetric conditions, and geographic position.

Phytoplankton production in western Lake Erie is controlled in general by the same factors listed for the ocean; however, the order of importance is not necessarily the same for the two situations. In this lake the direct factors, both primary and secondary, exhibit smaller annual variations than do the indirect factors. Several of these indirect factors are controlled by meteorological conditions and they appear to be largely responsible for the pronounced annual variations in phytoplankton production observed in this body of water.

One conspicuous difference between the physical conditions in 1942 and those in previous years was the indirect factor of river discharge. It was high and resulted in the initiation of one of Lake Erie's periodic high water stages. The lake level rose 2.38 ft. from March to the annual maximum in June, most of which was caused by a greater inflow of water from the upper Great Lakes, but some of the increase was due to increased discharge of the rivers in the southwest drainage area. During the entire year the lake level was higher than in any of the previous years thus far studied, and it is thought that this increase in volume affects lake metabolism through a general lowering of water temperature, a more rapid eastward flow of water, and an altering of the concentration of chemical compounds.

Water from the lakes above is colder than that in Lake Erie (Horton & Grunsky 1927); therefore, the greater the flow from the upper lakes the lower will be the temperatures in western Lake Erie. It seems that the lower water temperatures during 1942 can

be attributed in general to this greater inflow of water from the lakes above. That the volume of flow from the upper lakes is not the only factor affecting water temperatures in this lake is shown by the fact that during March and early April, at which time the lake level increased most rapidly, the water temperatures in Lake Erie were higher than for a corresponding time in other years. These high temperatures probably were due to the early disappearance of the ice cover accompanied by strong winds which warmed the water. Another factor that may have contributed to these higher water temperatures in March was the heavy discharge by the rivers in the southwest drainage area. Water from these rivers is warmer than the lake water (Horton & Grunsky 1927, and unpublished data at this laboratory); therefore, this unusually large volume of discharge could have increased the lake temperatures.

Most of the water that flows into Lake Erie by tributaries or from the lakes above enters at the western end and leaves the lake through the Niagara River at the east end. This eastward flow of water is continuous except for temporary interruptions by seiches. The rate of eastward flow increases with increased lake levels; therefore, during most of 1942 the water flowed eastward more rapidly than it did in the preceding year. The general results of this on phytoplankton production are not clear, but there is evidence that it tended to reduce the size of the standing crop. In other words the slower the rate of eastward flow the greater the length of time a given mass of water will remain in the shallow productive portion of this lake, and consequently the larger will be the standing crop. The general effects of increased lake level on the spring phytoplankton population of 1942 are obscured by the more drastic effects of high turbidities. The shape of the graph that represents the the autumn pulse, however, indicates that the level maintained from mid-September until late November may have been due in part to this effect of lake level.

The decrease in concentration of inorganic-N in 1942 as compared with 1939 and 1940, may also have resulted from the increase in river discharge in 1942. The relationship between fluctuations of the inorganic-N concentration of water samples taken from near the Bass Islands and the discharge from the Maumee and Portage rivers has been indicated. While data do not exist at present to show the quantitative relationship between river discharge and the concentration of nutrients in the river water, it seems permissible to outline the following hypothesis. The rate of removal and the quantity of nutrients removed from the soil by leaching and run-off depends upon the nature of the precipitation as well as the soil condition and would not be necessarily proportional to the amount of precipitation. Therefore, during the spring flood periods the concentration of nutrients in the river water might actually be less with a greater run-off. If the increased discharge from the tributaries of western Lake Erie in 1942 resulted in a diminished concentration of inorganic-N from this important source, then the relatively smaller concen-

tration of inorganic-N found near the Bass Islands may have been directly related to the greater inflow.

The increased discharge from the St. Clair-Detroit River in 1942, which amounted to more than 10,000 ft.³/sec., also might have contributed to the smaller concentrations of inorganic-N found. It is known (unpublished data at this laboratory) that the lake water from near the Canadian shore of western Lake Erie, which represents the water masses from the St. Clair-Detroit River, contains approximately one-half the concentration of inorganic-N, soluble phosphate-P, and silicate-Si that is found in the water near the Bass Islands. The apparent lack of relationship between the monthly mean flow from the St. Clair-Detroit River and the seasonal distribution in inorganic-N concentrations near the Bass Islands, seems to indicate that the decrease in concentration was due primarily to a diminished concentration of inorganic-N in the water from the southwest drainage area. Secondly, however, a dilution of the nutrient richer masses of lake water from the southwest drainage area by the masses of lower nutrient content from the upper Great Lakes might have been of importance. A more comprehensive knowledge of the total content of various nutrients in western Lake Erie plus a knowledge of the total contribution of these nutrients by the tributaries would determine whether the concentrations of nutrients are controlled by paralimnetic processes as has been indicated or by limnetic processes. Such a program is under way at present.

The influence of meteorological factors upon some of the physical and chemical conditions found for western Lake Erie in 1942 has been discussed. The effect of these conditions on phytoplankton production will be considered in the remaining paragraphs.

Considerable significance has been attached to the importance of nutrients in controlling phytoplankton production. Atkins (1923) has suggested that phosphorus is a limiting factor of phytoplankton production in the sea. Yoshimura (1932) has shown that phosphorus may be a limiting factor of phytoplankton growth in Takasuka Pond, Japan. Some of the Wisconsin workers (Juday, Birge, Kemmerer, & Robinson 1927; Juday & Birge 1931; and Tressler & Domogalla 1931) found no evidence that phosphorus was a limiting factor of phytoplankton growth in the lakes which they studied. Working with Linsley Pond, Riley (1940) considered the influence of both nitrate-N and phosphorus on phytoplankton growth, and he found that the phosphorus content of the water was more significantly correlated with increases in phytoplankton one week later than was the nitrate content. However, both of these nutrients seemed to effect some degree of control. Hutchinson (1941) concluded from enrichment of Linsley Pond water that nitrogen was more effective in producing an increase in phytoplankton, as judged by an increase in the concentration of chlorophyll, than was phosphorus, but that both of the elements must be present before other chemical limitations occur. In a later paper Hutchinson (1944) stated that for most small

lakes all nutrients necessary for phytoplankton growth probably were present in excess except nitrogen and phosphorus. Riley (1943) has attempted to clarify the complex situation which has arisen around factors controlling phytoplankton growth. Limiting factors are defined by him in the following manner. "If a change in a particular factor or group of factors in an otherwise controlled environment produces an increase in the growth curve of the species or association in that environment, the factor or factors are said to be limiting. The degree of limitation can be expressed as the difference between the original growth curve and the maximum curve obtainable by changing factors." The obvious difficulty in applying this to the consideration of chemical limitation of phytoplankton production in western Lake Erie is that the environment is not controlled. In the three years for which both phytoplankton and inorganic-N data are available, no occasion occurred in which a change in the numbers of phytoplankton could be attributed directly to a change in the concentration of inorganic-N. Riley's data on the growth, in the laboratory, of a pure culture of *Nitzschia closterium* indicate that concentration of nutrients do not alter the rate of growth but rather the length of the logarithmic growth period, and that cessation of logarithmic growth coincides with exhaustion of the nutrient supply. He found, however, that physical factors could reduce the growth rate, that is, a decrease in light intensity could change a population from a "state of active growth to senescence" long before it would otherwise occur. Inorganic-N data for western Lake Erie show that smaller concentrations of this element were present in the water during 1942 than in 1939 or 1940, yet the rate of growth of the spring populations was essentially the same, especially in 1939 and 1940. The magnitude of the spring crop in 1939, 1940, and 1942 seemed to depend upon physical factors, since a decrease in light intensity due to an increase in the amount of suspended material coincided with the abrupt termination of each pulse. By contrast to others years, the spring pulse of 1941 (Chandler 1944) represents the maximum population so far measured, and this occurred under the most ideal physical conditions so far observed. It is possible that chemical limitation played an important role during this season since one source of nutrients, water from the southwest drainage area, was limited by a relatively small river discharge. Unfortunately no chemical analyses of the water were made in 1941. If chemical limitation did occur in the spring of 1941, it is the only instance of this kind for the four springs. The case for chemical limitation of vernal phytoplankton production during 1939, 1940, and 1942 may be summarized by saying that during these seasons a more than adequate supply of nutrients appeared to exist for maximum phytoplankton production with the prevailing physical conditions.

It should be emphasized that during all but one of the spring periods so far investigated one genus

of diatoms, *Asterionella*, has predominated. The one exception was in 1940 when a large *Synedra* population coexisted with the *Asterionella* population. The occurrence of the same genus in a varying environment will facilitate the future study of factors controlling vernal phytoplankton production through a comparison of the inter-annual variations of the same factor or group of factors.

During autumn phytoplankton pulse periods the relative percentages of diatoms, greens, and blue-greens vary more widely from year to year than they do in the spring. In 1939 and again in 1941 diatoms comprised less than 50 percent of the units counted during autumn, while in 1938, 1940, and 1942 more than 75 percent of the units were made up by diatoms. The autumn pulse of 1942 when resolved to its components shows that no one genus of phytoplankton dominated throughout the entire period. Instead there occurred in succession several small pulses each composed of different genera. Usually the earliest stage of the autumn pulse is predominated by blue-green algae, and this is followed by ascendancy of the diatom population in September. The diatom population is also a mixture of several genera. In 1942 the first three peaks (Fig. 2 C) were due primarily to *Melosira* and the last peak to *Fragilaria*. The intra- and inter-annual variations in the composition of phytoplankton make it more difficult to determine the factors which affect production.

In another part of this paper it was noted that the smallest concentrations of inorganic-N have been found during August, September, and October of each year. It is possible that during this period of reduced supply the magnitude of the phytoplankton population may be influenced by the lower concentrations of nutrients. Certain data indicate, however, that this factor is but one of a series controlling autumn pulses. In comparison to 1939 and 1940 there was a smaller concentration of inorganic-N during all of 1942 but especially in the second half of the year. The autumn pulse of 1940 was controlled by excessive turbidity and therefore is not comparable to the autumn pulses of 1939 and 1942. The phytoplankton crops during the autumns of 1939 and 1942 were quite similar in quantity, and yet the inorganic-N content of the lake water analyzed in 1942 was less than 50 percent of that found in 1939.

In contrast to spring periods, when the early stages of the phytoplankton pulse frequently occur beneath an ice cover which controls to some extent the mixing of the lake water by wind, much of the phytoplankton production during autumn is accompanied by frequent storms. Chandler (1944) has emphasized the importance of storms during the autumn months. The storms come from all quarters. But many of them come from the northwest. Such storms would force a more complete mixing of the water from the northern half of western Lake Erie with that near the Bass Islands. In addition to the smaller concentrations of nutrients found in the northern part of this portion of the lake, the water contains a somewhat smaller phytoplankton population. The more

complete mixing of these two characteristically different masses of water during the storm periods no doubt influences the nature of the phytoplankton population measured near the Bass Islands.

The complex nature of the factors affecting autumn phytoplankton production has been indicated. Computation of the absolute growth rate of the *Melosira* population during its three periods of rapid growth in the autumn of 1942 shows that the rate is nearly constant. The *Fragilaria* population has a somewhat lower absolute growth rate, but this could easily be a generic character rather than the results of an altered environment. The relatively constant growth during the pulse can be interpreted from Riley's findings to indicate rather constant physical conditions. Turbidity was not the controlling factor of phytoplankton growth in the autumn of 1942 to the same extent that it was in the spring, since weekly mean values did not exceed 20 ppm. While the level of the standing phytoplankton crop was quite low, it was maintained for a long period of time so that the size of the autumn crop was moderately large. Since the concentration of nutrients presumably does not alter the rate of growth but only the duration of the logarithmic phase, and since the principal factor of physical control, light, was relatively constant, it is possible that the several abrupt decreases in the phytoplankton curve were caused by the lower concentrations of inorganic-N or some other nutrient. It is also possible that the eastward flow of water and the storm-induced mixing of lake water from the several areas of western Lake Erie having known biological, chemical, and physical differences account for some of the abrupt changes observed in the 1942 autumn phytoplankton curve.

SUMMARY

1. The phytoplankton in western Lake Erie and the limnological and meteorological conditions related to its annual abundance have been studied for the fourth consecutive year.

2. Each year the quality and quantity of phytoplankton have been different, and in an attempt to account for these differences various limnological and meteorological factors known to affect this phytoplankton have been measured and evaluated.

3. Phytoplankton production in 1941 was the greatest of the four years studied; therefore, the phytoplankton and the limnological and meteorological conditions of 1941 are used as a standard for comparison.

4. Water temperatures varied from a winter minimum of 0.3° C. to a summer maximum of 26.4° C. The annual heat budget was 19,764 g-cal. per cm.² which is about 3 percent lower than in 1941. The water began to warm earlier in 1942 than in 1941, but the rate of heat loss during the autumn of the two years was about the same. The amount of heat stored in the water at a given time varies widely from year to year.

5. An ice cover formed in the island region on January 5 and it remained intact until March 9. The ice

attained a maximum thickness of 12 inches and it was relatively free from snow. It covered a smaller portion of western Lake Erie than it did in 1941.

6. Solar and sky radiation received at Put-in-Bay amounted to 117,492 g-cal. per cm.² in 1942; this is about 7 percent less than that received during 1941.

7. More tributary water entered this end of the lake in 1942 than in 1941. Discharge from the St. Clair-Detroit River was about 7 percent greater in 1942 and that from the southwest drainage area was about 200 percent greater. The effects of this increased river discharge were evident from the high spring turbidities and the increased lake level of 1942.

8. Precipitation in the southwest drainage area was about 36 percent greater in 1942 than in 1941, and run-off was about 249 percent greater.

9. The 1942 annual mean level of Lake Erie was 571.78 ft. which is 0.58 ft. higher than the annual mean of 1941. A difference of 2.48 ft. existed between the lowest and highest weekly means during the year in western Lake Erie. The effects of these differences in lake level on heat budgets, water movements, and concentration of nutrients are considered.

10. Seiches at Put-in-Bay varied in amplitude from 0.3 ft. to 5.9 ft. in 1942. There were 17 seiches with an amplitude of 2.0 ft. or greater and most of these occurred during late autumn and early winter.

11. Lake turbidities varied from 3 ppm. to 160 ppm. In general, spring turbidities were much higher in 1942 than in 1941, and this may be accounted for by greater river discharge in 1942. Turbidities are progressively lower down-lake from Toledo to Cleveland; this is due to the distribution of tributary streams and to the factors of dilution and sedimentation.

12. Depths to which 1 percent of the surface light penetrated during spring varied from 2.0 to 3.0 m.; during autumn it varied from 2.0 to 5.0 m.

13. Concentrations of soluble phosphate-P varied during the latter half of 1942 from 1 to 8 µg per 1. An average of 29 percent of the total-P was in this form. The concentration of organically combined P, which ranged from 2 to 26 µg per 1, usually varied directly as the number of phytoplankters. The available data indicate that the phosphorus cycle in western Lake Erie is not a closed one; paralimnetic factors apparently play a major part in determining the concentrations of soluble phosphate-P which are found. Pelometabolism does not enter greatly into the phosphorus economy because of the persistent oxidized zone at the mud-water interface.

14. Total inorganic-N concentrations, which varied from 12 to 1,520 µg per 1 during 1942, were determined from the concentrations of ammonia-N, nitrite-N, and nitrate-N of the lake water. Nitrate-N comprised between 48 and 97 percent of the inorganic-N. The largest concentrations of nitrate-N, both absolute and relative with respect to total inorganic-N, occurred during the spring and late autumn months. Data for 1939 and 1940 show that this is a recurrent phenomenon, and that the winter months also may be characterized by relatively large concentrations of

nitrate-N. The absolute concentrations of ammonia-N and nitrite-N were also highest during the spring and autumn months of 1942, but the relative concentrations of these compounds were largest during July, August, and September. River discharge apparently controls to an appreciable extent the seasonal distribution of nitrate-N in the one part of western Lake Erie studied, but to a lesser extent the seasonal distribution of ammonia-N and nitrite-N.

15. Data indicate that the concentrations of nitrate-N in the lake water near the Bass Islands varies directly as, but not necessarily in proportion to, the river discharge from the southwest drainage area of western Lake Erie. It seems that flow of water from the upper Great Lakes through the St. Clair-Detroit River is not so closely related. The tributaries of western Lake Erie, therefore, are an important source of the non-conservative elements, especially since the morphometry of western Lake Erie does not permit the accumulation of deep water reserves of these elements.

16. The size of the 1942 spring phytoplankton crop was only 19 percent of the 1941 spring crop. It occurred from early February to mid-April with a maximum of 459,000 units per l in early March. It was brought to a premature termination by high lake turbidities caused by river discharge. Composition of this crop was 94 percent diatoms, 4 percent greens, and 2 percent blue-greens. *Asterionella* alone composed about 81 percent of the entire spring crop.

17. The size of the autumn crop in 1942 was 14 percent smaller than the 1941 autumn pulse. It began in mid-July and terminated in late November. Duration of this pulse was greater than any other observed in previous years. The pulse was composed of 76 percent diatoms, 20 percent blue-greens, and 4 percent greens. The diatom crop during the autumn of 1942 was larger than any in the three previous years; *Melosira* composed about 85 percent of this large pulse.

18. At Cleveland, diatoms composed 98 percent of the spring phytoplankton pulse and about 94 percent of the autumn pulse. *Asterionella* and *Melosira* were nearly equal in abundance and together they composed 77 percent of the spring diatoms. *Melosira* composed about 75 percent of the autumn diatom crop.

19. Studies of the phytoplankton at Put-in-Bay and at Cleveland during 1942 confirm earlier observations in respect to the following: (1) in general both spring and autumn pulses begin earlier at Put-in-Bay than at Cleveland, but the overall-duration is about the same; (2) composition of the spring phytoplankton is very similar at the two stations; (3) greens and blue-greens compose a greater percentage of the autumn phytoplankton at Put-in-Bay than at Cleveland; and (4) annual variations in abundance are greater at Put-in-Bay than at Cleveland.

20. The seasonal abundance of the more common genera of greens, blue-greens, and diatoms are given for collections made at Put-in-Bay.

21. Physical factors rather than chemical factors usually control vernal phytoplankton production in western Lake Erie. During the spring of 1942 high turbidities of the lake water, masking the influence of other physical factors, appear to have controlled the size of the phytoplankton crop.

22. Autumn phytoplankton production does not seem to be controlled by one condition as is usually the instance in spring periods. A comparison of the 1942 autumn environment with that of the autumn periods of earlier years has been made. The conditions which might have effected the reduced autumn 1942 phytoplankton crop are thought to be the increased rate of eastward movement of the lake water; storm-induced mixing of areas of western Lake Erie which exhibit physical, chemical, and biological differences; and perhaps the reduced concentration of nutrients.

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